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Proceedings of the VIIth International Symposium on Dental Morphology

edited by

D. E. RUSSELL
J.-P. SANTORO
D. SIGOGNEAU-RUSSELL

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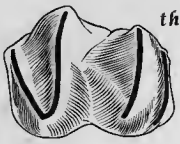

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Preface

This volume contains most of the papers presented at the VII[th] International Symposium on Dental Morphology, held in Paris from May 20 to 24, 1986. Out of the six preceding symposia, four were published: the first (Denmark, 1965) appeared in the *Journal of Dental Research*, (1967); the second (London, 1968) was edited by A. A. Dahlberg (*Dental Morphology and Evolution*, 1971); the fourth (Cambridge, 1974) by P. Butler and K. A. Joysey (*Development, Function and Evolution of Teeth*, 1978) and the fifth (Finland, 1979) by B. Kurtén (*Teeth: Form, Function and Evolution*, 1982). The third (Belgium, 1971) and the sixth (Iceland, 1983) unfortunately were not published.

Contrary to what their title would lead one to believe, these symposia, and in particular the present one, greatly exceed the limits of merely dental morphology, as they have brought together specialists of numerous disciplines: embryology, genetics, histology, paleontology, physiology and zoology. Indeed, teeth lend themselves eminently well to multidisciplinary studies, their multiple properties rendering them organs of unique quality; and it is not the least of the interests of these symposia that they permit the confrontation of data that would otherwise be restricted to specialized journals.

We hope that the authors, whom we thank for their patient collaboration, will find in this volume a refleetion of the stimulating atmosphere of the symposium, and that its readers will discover material to nourish or to valorize their future research.

Like any other organ, teeth are dependent on the hereditary material. The relationships between phenotype and genotype in the dentition were the subject of two presentations. G. Townsend, L. Alvesalo, B. Jensen and M. Kari, by a study of chromosomal aneuploidies, show that, in man, the sexual chromosomes play a role in cellular growth and differentiation: Y favors growth by affecting the thickness of enamel and dentine; X has an effect on enamel deposition. Tooth variables concerning size and bilateral asymmetry, regarded as reflections of genetic variance, were examined by R. S. Corruccini, K. Sharma and R. H. Y. Potter. The novelty of their approach is that it combines studies made on twins from the United States with those from Punjabi, India.

What genetic material controls is odontogenesis. Embryological research on tooth patterning has sometimes led to contradictory results. The study by B. Westergaard is particularly welcome, as it concentrates on several reptile species and shows first that, based on the position and the time of appearance of tooth germs, a generalized pattern can be recognized, allowing homologies between these species; second, the absence of alternance in the embryonic dentition: the developmental scenario advocated by B. Westergaard links tooth position with jaw growth (Tooth Position Theory). The previous theories would be the result of misinterpretation. The caution to be exerted on embryological studies, as emphasized by B. Westergaard, is exemplified by N. Ahmad and J. V. Ruch who show that, in *in vitro* studies of mouse teeth, there is a considerable slowing of cellular growth and proliferation with respect to the same phenomena *in vivo* due to lengthening of the cellular cycle, perhaps by intervention of extracellular factors.

The ontogenetic steps lead to the realization of functional teeth, knowledge of which starts with that of dental tissues. Among the latter, enamel and its allies constitute a very rich material for analysis. In lower vertebrates, in fact, the nature of enameloid tissues is still disputed; F. J. Meunier, M. Gayet, J. Géraudie, J.-Y. Sire and L. Zylberberg show that ganoine, covering scales and

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odontodes in primitive extant actinopterygian fishes, is produced by the epithelium and as such is a true enamel. As for mammalian enamel, it has become a favorite subject both for anatomists and paleontologists and contains the potential for use as a systematic tool. For example, A. Sahni and K. S. Lester consider that enamel tubules, if properly revised and quantified, would be of useful taxonomic value, and they present their distribution in therapsids, multituberculates and marsupials. R. M. Frank, D. Sigogneau-Russell and J. Hemmerlé, on the other hand, try to clarify the contradictions resulting from the studies made of triconodont enamel: it does seem that a stage of preprismatic enamel preceded that of true prismatic enamel in the different early mammalian lineages. At the other end of mammalian evolution, proboscidean enamel has been investigated by P. Bertrand, who recognizes, by means of a diversified methodology, three fundamental types in primitive members of the group and who proposes linking the Deinotheriidae and Barytheriidae on the basis of their very peculiar enamel organization. Y. Kozawa, H. Mishima and T. Sakae, for their part, relate the complicated structure of the *Elephas* molar to its enamel complexity. From a more generalized point of view, H.-U. Pfretzschner makes use of a theoretical model to appreciate the effects of stress on the enamel and its consequent fissuration. Hunter-Schreger bands appear to be an adaptation reinforcing the enamel against the most critical horizontal forces. This is confirmed by W. von Koenigswald who detects, in enlarged front teeth of several orders of mammals, two more ways of reinforcing the enamel and protecting it from fissuration. Finally, R. Bouchez and his colleagues propose the use of various physicochemical data to elucidate the process of fossilization of dental tissues and to date fossil enamel up to three million years old. From these punctual studies, enamel structure appears to be a mine of information whose reserve is still far from exhausted.

The dentition taken as a whole is no less inspirational for the light it throws on evolutionary phenomena. Again, the mammalian dentition, with its infinite variation, has been the subject of most of the research done, while that of the lower vertebrates has often been neglected. In consequence, analyses such as those of M. M. Smith on Palaeozoic lungfishes and R. Lund on Carboniferous holocephalians are of particular interest. The first author starts from the fact that there is no consensus on the primitive state of the dentition in lungfishes. After establishing a proper distinction between denticles and teeth and showing the value of this distinction in the demonstration of relations, she differentiates two types of dental plates and on these she proposes a new classification of lungfishes possessing them. It is also on the basis of dental plates that R. Lund demonstrates a cladistic relationship between the different groups of holocephalians.

Among mammals, one of the most frequent of the evolutionary phenomena is that of convergence; it is illustrated in this volume by two papers. J. F. Bonaparte gives an example of the early development of hypsodonty in a Cretaceous mammal, perhaps the response to silica-containing food. The example given by R. Pascual, A. A. Carlini and L. J. M. De Santis is still more striking: the same morphogenetic paths led to true placental rodents as well as to two independant lineages of rodent-like marsupials, one during the Paleogene and the other during the Neogene.

The evolutionary processes themselves can be revealed by research on teeth. J. Agusti, in a stimulating paper on dental evolution in Quaternary to Recent island forms, indicates that phases of insularity seem to demonstrate the punctuated equilibria mode of evolution. Finally the evolutionary significance of dental morphology has been explored by several authors. H. Kamiya and H. Taruno are also concerned with insular mammals, but the islands this time are Japanese, not Mediterranean, and the animals Proboscidea, not rodents. Basing their work on the tooth structure of three genera, they proceed to the phylogenetical conclusion that *Eostegodon* from the Japanese Miocene is ancestral to *Stegodon*. The latter and *Stegolophodon* are common in the late Tertiary and Quaternary deposits of southeast Asia. The dental morphology of two living groups of mammals, carnivores and bats, has been dealt with in quite differing fashions by M. Wolsan and by P. Sevilla and N. Lopez-Martinez. M. Wolsan has analyzed in great detail the polymorphism found in the first upper molar of the mustelid *Martes* and suggested that his findings shed light on the evolution of the lineage; he adds that population studies of this sort, supported by statistical treatment, could

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also contribute to an understanding of speciation within the genus. Also making use of statistical methods, P. Sevilla and N. Lopez-Martinez show that, in Chiroptera at least, dental characters have as high a diagnostic value as external and skeletal features.

Two peculiar cases of dental morphology have been presented by B. Lange-Badré and P. Mein. The first author has described and interpreted functionally a creodont molar from the early Tertiary, whose morphology and functional mechanisms are singularly different from those usually encountered in a carnivorous mammal. P. Mein, on the other hand, has been confronted with a rather bewildering variety of strange Miocene rodent teeth. In this sampling, he cites specimens that range in unexpected features from a single anomaly to those that are totally aberrant; some of the latter probably have a chromosomal origin and consequently could illustrate phyletic affinities.

Human dentitions and their variability lend themselves admiringly well to morphologic studies. From Neolithic burials in the Baluchistan Province of Pakistan, J. R. Lukacs reports on the first finding of skeletal remains that provide information on the dental characteristics of the early agriculturists of the Indus Valley. These data can be compared with those of other Chalcolithic populations in western India who may be their descendants, and provide matter for speculation on subsistence techniques and ecological settings. On the other side of the world, G. R. Scott, S. Street and A. A. Dahlberg have examined tooth crown trait variables in five Yuman speaking Indian tribes of the American Southwest. A positive relationship could be established between the results of this analysis and those from other disciplines, such as linguistics, genetics and physical anthropology; it thus becomes apparent that comparative dental morphology has an important role to play in deciphering the prehistory of the region. Among the general problems met with in the human dentition, A. A. Dahlberg has lain heavy emphasis on variability. The latter affects the form, size and structure of teeth and responds to aggressions from the environment. The author stresses that, for anthropological studies in particular, the importance of variation analyses cannot be overestimated.

The last theme envisaged in this volume concerns some basic as well as more esoteric aspects and ramifications of the relations between diet and tooth wear. P. M. Butler and J. R. E. Mills plunge into the depths of therian origins; the former points to a morphological and functional parallelism between docodont and leptictid insectivores with the development in both of the crushing function. J. R. E. Mills, in a more general presentation, traces the first steps in dental evolution that permitted real chewing, a character distinguishing mammals from reptiles. It is shown that the complexities of mastication entail not only the flexibility of a dentary-squamosal articulation but also morphologically more complicated teeth with precise occlusion. Modifications in this occlusion are followed from the first therian mammals, through early primates to *Gorilla* and man. The mechanisms of the transition from insectivory to herbivory at the Cretaceous-Tertiary boundary are explored by J. M. Rensberger. He emphasizes the structural modifications that have taken place and that have led to a change in the breaking down of food: in insectivorous animals the chewing system was dominated by shearing, in herbivores by compressive action. A well documented proposal for determining tooth volume and hypsodonty indices in ungulates is made by C. M. Janis. She furthermore postulates that these two factors are influenced more by habitat preference than by dietary preference and uses the data on living ungulates as a base upon which to interpret extinct relatives.

It is again with hominids that this section on the relation between dentition and diet concludes. P. Smith makes a demonstration of attrition patterns in three species of australopithecines and proposes a simple, reliable method for quantifying these patterns, which reflects functional adaptations and is related to modifications of tooth size. P.-F. Puech shows, by a microscopic study of wear in incisors and cheek teeth that, of the hominids of Olduvai, *Homo habilis* fed to a considerable degree on papyrus or cereals, while *Australopithecus boisei* tended more to consume root vegetables; he concludes that this alimentary separation probably permitted their cohabitation. The two following articles deal with contemporary man: an analysis of occlusal and interstitial tooth wear in three groups of Bushmen was made in depth by J. F. van Reenen and S. G. Reinach. By a series of well documented observations, they show that

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differences in patterns of occlusal and interstitial wear are due to the coarseness of the diet, masticatory preference areas and the individual chewing patterns. The function of human incisors in processing food is examined by J. W. Osborn, F. A. Baragar and P. E. Grey, using imaginative techniques. The role of tilt in these incisors is carefully analysed and is shown to be of vital importance in cutting food ; this function clearly takes precedence over other things one can do with spatulate incisors. Terminating, M. Fortelius presents an arcane approach to chewing in general, in which he suggests that an isometric relationship exists between the amount of food comminuted per chew and the volume of food enclosed between the cheek teeth, rather than directly with the occlusal area. Other relationships are also considered.

As shown by the diversity of the subjects treated in this volume, the potential for study contained in the dental organs obviously remains great. For instance, research on wear phenomena in mammals is badly needed, the functional significance of morphologic variation is poorly understood, the moment and mode of appearance of certain structures are still vague, and the all too frequent neglect of teeth in lower vertebrates is to be rectified; the latter brings to mind discussions concerning the modalities of dental replacement that continue without definitive resolution. We anticipate the treatment of these and other problems in contributions to future symposia.

In conclusion, the organisors of this symposium express their gratefulness to the Direction de la Coopération et des Relations Internationales for having furnished financial support for these meetings, and to Professor P. Taquet, Director du Muséum national d'Histoire naturelle, whose enthusiasm and active aid were vital for both the organisation of the symposium and the publication of the ensuing proceedings. The acceptance of this work by Monsieur Y. Laissus, Directeur des Publications du Muséum, and the helpfulness of Dr. P. Bouchet, Editor of the Mémoires du Muséum, in facilitating the publication of this volume have been greatly appreciated. This note of thanks cannot end without expressing gratitude to all the participants, who made the symposium possible.

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JEAN-PIERRE SANTORO
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Source : MNHN, Paris

Préface

Le présent volume renferme la plupart des communications présentées au VII[th] International Symposium on Dental Morphology, tenu à Paris du 20 au 24 Mai 1986. Rappelons que sur les six symposia précédents, quatre ont fait l'objet de publications : le premier (Danemark, 1965) est paru dans le *Journal of Dental Research*, 1967 ; le second (Londres, 1968) fut édité par A. A. Dahlberg (*Dental Morphology and Evolution*, 1971) ; le quatrième (Cambridge, 1974) par P. Butler et K. A. Joysey (*Development, Function and Evolution of Teeth*, 1978) et le cinquième (Finlande, 1979) par B. Kurtén (*Teeth: Form, Function and Evolution*, 1982). Les troisième (Belgique, 1971) et sixième (Islande, 1983) n'ont malheureusement pas été publiés.

Contrairement à ce que pourrait laisser croire leur dénomination, ces symposia, en particulier celui qui fait l'objet de la présente publication, dépassent de beaucoup le cadre de la seule morphologie dentaire, puisqu'ils réunissent les chercheurs de nombreuses disciplines : embryologie, génétique, histologie, paléontologie, physiologie et zoologie. En effet les dents se prêtent éminemment, par leurs multiples propriétés qui en font des organes tout à fait à part, à des études multidisciplinaires, et ce n'est pas le moindre intérêt de ces symposia que de permettre la confrontation de données habituellement cantonnées à des revues spécialisées.

Nous espérons que les auteurs, que nous remercions pour leur patiente collaboration, retrouveront dans ce volume un reflet de l'atmosphère stimulante du symposium, et que tous les lecteurs y découvriront matière à alimenter ou valoriser leurs futures recherches.

Comme tout autre organe, les dents sont sous la dépendance du matériel héréditaire. Les relations entre le phénotype et le génotype dans la denture ont fait l'objet de deux communications. G. Townsend, L. Alvesalo, B. Jensen et M. Kari montrent, par l'étude des aneuploïdies chromosomiques et leur effet sur la taille et l'asymétrie bilatérale des dents, que, chez l'homme, les chromosomes sexuels jouent un rôle dans la croissance et la différenciation cellulaires: Y favorise la croissance en agissant sur l'épaisseur de l'émail et de la dentine ; X exerce une influence sur le dépôt de l'émail. Ces deux variables que sont la taille et l'asymétrie bilatérale des dents sont donc le reflet de la variance génétique : R. S. Corruccini, K. Sharma et R. H. Y. Potter approchent ce même sujet de façon originale en combinant les études réalisées sur des jumeaux nord-américains et indiens Punjabi.

L'influence du matériel génétique s'exerce durant l'ontogénèse. Or les recherches embryologiques portant sur l'organisation de la denture ont parfois conduit à des résultats contradictoires. L'étude de B. Westergaard est donc particulièrement bienvenue, elle qui porte sur plusieurs espèces de reptiles et atteste premièrement qu'on peut, en se basant sur la position et le moment d'apparition des germes dentaires, établir des homologies entre espèces, et deuxièmement qu'il n'y a pas d'alternance régulière dans la dentition embryonnaire ; le scénario ontogénétique retenu par B. Westergaard établit un lien entre la position des dents et la croissance de la mâchoire (Théorie de la Position des Dents). La prudence qui doit présider aux études embryologiques, telle que préconisée par B. Westergaard, est soulignée par N. Ahmad et J. V. Ruch qui signalent que, lors d'études *in vitro* des dents de souris, la croissance et la prolifération cellulaires sont considérablement ralenties par rapport aux mêmes phénomènes *in vivo*, en raison de l'allongement du cycle cellulaire dans lequel interviennent peut-être des facteurs extra-cellulaires.

Les étapes ontogénétiques conduisent à la

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réalisation de dents fonctionnelles, dont la connaissance débute avec celle de leurs tissus constituants. Parmi ceux-ci, l'émail et les tissus apparentés représentent un très riche matériel d'investigation. C'est ainsi que la nature des tissus énaméloïdes des Vertébrés inférieurs est encore sujette à discussion. Or F. J. Meunier, M. Gayet, J. Géraudie, J.-Y. Sire et L. Zylbelberg démontrent que la ganoïne, qui recouvre les écailles et les odontodes des Actinoptérygiens primitifs actuels au moins, est produite par l'épithélium et est en conséquence un véritable émail. Quant á l'émail mammalien, il est devenu le sujet de choix de nombreux zoologistes et paléontologistes qui tentent d'en faire un outil systématique. A. Sahni et K. S. Lester, par exemple, considérent que les tubules de l'émail, une fois convenablement révisés et quantifiés, présenteront une utilité taxonomique certaine ; une première mise au point de leur répartition chez les Thérapsides, Multituberculés et Marsupiaux est présentée. R. Frank, D. Sigogneau-Russell et J. Hemmerlé, quant á eux, tentent d'éclairer les résultats parfois contradictoires obtenus par divers auteurs sur l'émail des Mammifères triconodontes. A la suite de leur investigation, il apparaît qu'un stade d'émail préprismatique a précédé l'émail véritablement prismatique, et ce dans les différentes lignées de Mammifères primitifs. A l'autre extrémité de l'échelle évolutive mammalienne, l'émail des Proboscidiens a fait l'objet d'un travail de P. Bertrand qui reconnaît, par une approche méthodologique variée, trois types fondamentaux dans l'émail des membres primitifs du groupe et propose de rapprocher, sur la base de l'organisation trés particuliére de leur émail, les Deinotheriidae et les Barytheriidae. Y. Kozawa, H. Mishima et T. Sakae, de leur côté, mettent en relation la structure compliquée de l'émail et de la morphologie de la molaire d'*Elephas*. D'un point de vue plus général, H.-U. Pfretzschner a recours á un modéle théorique pour apprécier les effets du stress sur l'émail et sa fissuration. Les bandes de Hunter-Schreger se révélent être un caractére adaptatif dont l'effet est de renforcer l'émail contre les tensions horizontales les plus critiques. Cette conclusion est confirmée par W. von Koenigswald, qui détecte en outre, sur les grandes dents antérieures de plusieurs ordres de Mammifères, deux autres modes de renforcement de l'émail et de protection contre la fissuration. Finalement, R. Bouchez et ses collégues ont soumis l'émail de plusieurs Vertébrés continentaux á diverses analyses physiques qui les conduisent á élucider certains aspects du processus de fossilisation des tissus dentaires et á dater l'émail jusqu'á 3 millions d'années. Il ressort clairement de ces quelques études ponctuelles que la structure de l'émail renferme une mine d'informations qui sont encore loin d'être totalement exploitées.

La denture prise dans son ensemble n'est pas moins riche de potentialités, particuliérement dans la mesure oú elle jette quelque lumiére sur les phénoménes évolutifs. Lá aussi c'est la denture des Mammifères et ses infinies variations qui ont fait l'objet de la plupart des recherches, tandis que les Vertébrés inférieurs restent trop souvent négligés á cet égard. En conséquence les analyses telles que celles de M. M. Smith sur les Dipneustes du Paléozoïque et de R. Lund sur les Holocéphales carbonifères sont particuliérement appréciées. M. M. Smith, aprés avoir instauré une distinction nette entre denticules et dents, et montré l'importance de cette distinction dans l'établissement des relations de parenté, propose de distinguer deux types différents de plaques dentaires, sur lesquelles elle fonde une nouvelle classification des Dipneustes pourvus de plaques dentaires. C'est aussi sur la base de plaques dentaires que R. Lund réalise une classification cladistique des différents groupes d'Holocéphales carbonifères. Il est á souhaiter que de telles études servent d'exemple et d'inspiration à de nombreuses autres.

Dans la denture des Mammifères, un des phénoménes évolutifs le plus couramment rencontré est le phénoméne de convergence, illustré dans ce volume par deux articles. J. F. Bonaparte fait état d'un cas précoce d'hypsodontie chez un mammifére crétacé, en réponse á une nourriture siliceuse. L'exemple fourni par R. Pascual, A. A. Carlini et L. J. M. De Santis est encore plus frappant, puisque c'est le même parcours morphogénétique qui conduit à des dentures similaires d'une part chez les vrais Rongeurs placentaires, d'autre part et indépendamment dans deux lignées de Marsupiaux, l'une durant le Paléogéne et l'autre durant le Néogéne.

Les processus évolutifs eux-mêmes peuvent être cernés par l'étude des dents : pour J. Agustí, l'évolution dentaire chez les Rongeurs insulaires du Quaternaire au Récent s'accorde bien avec le modèle des équilibres ponctués. Enfin la significa-

Source : MNHN, Paris

tion évolutive de la morphologie dentaire est explorée par plusieurs auteurs. H. Kamiya et H. Taruno s'intéressent également aux formes insulaires, dans des îles japonaises et non plus méditerranéennes, et chez les Proboscidiens. Se fondant sur la structure dentaire de trois genres, ils concluent à l'existence d'une relation phylogénétique entre *Eostegodon* du Miocène japonais et *Stegodon*, forme commune, avec *Stegolophodon*, dans le Tertiaire tardif et le Quaternaire d'Asie du Sud-Est. M. Wolsan analyse dans le plus grand détail le polymorphisme observé sur la première molaire supérieure chez six espèces du genre *Martes*, analyse qui éclaire l'évolution de la lignée et pourrait élucider aussi le processus de spéciation à l'intérieur du genre. De leur côté P. Sevilla et N. Lopez-Martinez démontrent, par une méthode statistique, que, chez les chauves-souris, les caractères dentaires ont une valeur diagnostique aussi significative que les facteurs externes et squelettiques. Enfin B. Lange-Badré et P. Mein présentent deux cas très particuliers de morphologie dentaire : la première étude porte sur un Créodonte du début du Tertiaire, dont la molaire inférieure diffère notablement par sa morphologie et son fonctionnement de celles rencontrées habituellement chez les Mammifères carnassiers. La seconde nous confronte à quelques dents de Rongeurs miocènes de morphologie aberrante, aberrations qui vont de la simple anomalie à une configuration totalement énigmatique, dont certaines ont probablement une origine chromosomique et peuvent par conséquent illustrer des parentés phylétiques.

La denture humaine et sa variabilité se prêtent éminemment à des études morphologiques. C'est ainsi que, dans des sépultures néolithiques situées dans la province du Baluchistan, Pakistan, J. R. Lukacs rapporte la découverte de restes squelettiques fournissant des informations sur les caractères dentaires des premiers agriculteurs de la vallée de l'Indus. Ces dentures sont comparées en particulier à celles d'autres populations chalcolithiques de l'Inde occidentale, qui en sont peut-être les descendants, et donnent de surcroît matière à un certain nombre de spéculations sur les techniques de subsistance et sur l'environnement. De leur côté, G. R. Scott, G. Street et A. A. Dahlberg ont examiné les variables morphologiques de la couronne dentaire dans cinq tribus indiennes de langue Yuman d'Amérique du Sud-Ouest. Les résultats peuvent être reliés à ceux émanés d'autres disciplines telles que la linguistique, la génétique et l'anthropométrie, témoignant du rôle important que joue l'examen comparatif de la morphologie dentaire dans la connaissance de la préhistoire. A. A. Dahlberg enfin met une emphase particulière sur la variabilité de forme, de taille et de structure que présentent les dents humaines en réponse aux agressions du milieu. L'auteur insiste sur le fait qu'on ne saurait exagérer l'importance des analyses de variabilité dans les études anthropologiques.

La dernière rubrique envisagée dans ce volume concerne le régime alimentaire tel qu'on peut le déduire de l'étude combinée de la morphologie et de l'usure dentaires, et ce même chez les Mammifères fossiles, aussi anciens fussent-ils. C'est ainsi que P. M. Butler et J. R. E. Mills plongent aux origines des thériens, le premier pour faire ressortir une convergence morphologique et fonctionnelle entre les docodontes et les insectivores lepticitides, avec développement dans les deux cas de la fonction d'écrasement. J. R. E. Mills, quant à lui, retrace les premières étapes de l'évolution dentaire qui ont permis, chez les Mammifères, une véritable mastication. Il montre que la réalisation de cette fonction suppose non seulement une articulation dentaire-squamosal flexible mais aussi une morphologie dentaire complexe avec occlusion. L'auteur suit les modifications de cette occlusion depuis les premiers Mammifères thériens, à travers les premiers Primates, jusqu'à l'homme. Les mécanismes de la transition du régime insectivore au régime herbivore à la limite Crétacé-Tertiaire sont démontés par J. M. Rensberger, qui met l'accent sur les modifications structurales qui sont intervenues et ont conduit à un changement dans la façon de désagréger la nourriture, depuis les insectivores, chez qui domine l'action coupante, jusqu'aux herbivores où domine l'action de compression. Précisément chez les herbivores (Ongulés), C. M. Janis offre une méthode de calcul des indices du volume dentaire et de l'hypsodontie. Elle suggère ensuite que ces deux facteurs sont influencés davantage par les préférences écologiques que par les préférences alimentaires, et se fonde sur les données obtenues sur les ongulés récents pour interpréter leurs parents fossiles.

C'est encore avec les hominidés que se termine cette section sur la relation entre denture et régime. P. Smith étudie le mode d'attrition chez trois espèces d'Australopithèques et développe

Source : MNHN, Paris

une méthode simple et fiable pour quantifier ce phénomène, qui reflète des adaptations fonctionnelles, et se relie aux modifications de la taille des dents. P.-F. Puech, par un examen microscopique de l'usure des incisives et des dents jugales des hominidés d'Olduvai, suggère qu'*Australopithecus boisei* consommait plutôt des racines végétales tandis qu'*Homo habilis* se nourrissait largement de Cypéracées et de Graminées, et que c'est probablement cette ségrégation alimentaire qui a permis la cohabitation des deux espèces. Les deux articles suivants traitent de l'homme moderne : une analyse de l'usure occlusale et interstitielle dans trois groupes de Bushmen est réalisée par J. F. van Reenen et S. G. Reinach, qui fournissent une série d'observations bien documentées faisant apparaître que les différences dans le mode d'usure occlusal et interstitiel résultent de la nature de la nourriture, des surfaces masticatoires préférentielles et des modes individuels de mastication. J. W. Osborn, F. A. Baragar et P. E. Grey usent de techniques imaginatives pour illustrer le rôle des incisives humaines dans le processus de dilacération de la nourriture, d'où il ressort que l'inclinaison de ces dents est le principal facteur qui en fait des agents essentiellement coupants. Enfin M. Fortelius aborde le problème de la mastication en général, et suggère qu'il existe une relation isométrique entre la quantité de nourriture désagrégée par mouvement masticatoire et le volume de nourriture enfermé entre les dents jugales, plutôt que directement avec la surface occlusale, ce qui explique le paradoxe apparent entre la prédiction d'allométrie positive et l'observation d'isométrie pour les dents jugales par rapport à la taille du corps.

La diversité des sujets abordés témoigne que le potentiel d'étude des organes dentaires est loin d'être épuisé : c'est ainsi, pour ne citer que quelques exemples, que les études concernant les phénomènes d'usure chez les Mammifères sont encore peu nombreuses, la signification fonctionnelle des variations morphologiques mal comprise, l'époque et le mode d'apparition de certaines structures encore imprécis ; enfin les dents des Vertébrés inférieurs sont souvent négligées, et les modalités du remplacement dentaire y restent encore discutées. On peut espérer que les futurs symposia contribueront à leur tour à éclaircir ces problèmes.

En conclusion, les organisateurs de ce Symposium expriment leur reconnaissance à la Direction de la Coopération et des Relations Internationales pour avoir subventionné cette réunion, et au Professeur P. Taquet, Directeur du Muséum national d'Histoire naturelle, dont l'intervention fut primordiale tant pour l'organisation des Séances que pour la publication des communications dans les Mémoires du Muséum. Pour avoir accepté d'ouvrir cette série aux actes de notre Symposium, M. Y. Laissus, Directeur des Publications du Muséum, et M. P. Bouchet, Directeur des Mémoires, sont assurés de la vive gratitude de tous. Les éditeurs remercient enfin ceux de leurs collègues qui ont accepté le rôle ingrat de rapporteurs.

D. E. RUSSELL
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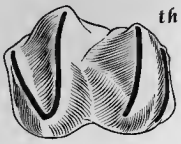
D. SIGOGNEAU-RUSSELL

Source : MNHN, Paris

EMBRYOLOGY AND GENETICS



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Patterns of Tooth Size in Human Chromosomal Aneuploidies

G. TOWNSEND, L. ALVESALO, B. JENSEN & M. KARI

ABSTRACT

Patterns of tooth crown size and asymmetry were determined for individuals with the following chromosomal aneuploidies: Down syndrome (DS), Klinefelter (XXY) syndrome, XYY males and Turner (XO) syndrome. Tooth size was generally increased in the presence of an additional X or Y chromosome, whereas loss of an X chromosome resulted in a reduction in tooth size. The most marked effect of the extra autosome in Down syndrome was a reduction in permanent tooth size but some deciduous teeth were larger than normal. Fluctuating dental asymmetry was increased in the XXY and DS groups, reflecting a disruption in developmental stability, but this was not apparent in the XO group.

Both the sex chromosomes appear to exert a direct growth-promoting influence on tooth size. The Y chromosome seems to affect enamel thickness, possibly by regulating amelogenesis, and also dentine thickness, perhaps by modifying cellular proliferative activity. The main role of the X chromosome appears to involve regulation of enamel deposition. The dental findings in DS are consistent with a general reduction in cellular mitotic activity in this condition. The effects of chromosomal aneuploidies on tooth size were not uniform throughout the dentition and this may reflect variations in timing and rate of cell proliferation and differentiation between developing tooth germs.

RÉSUMÉ

Les modifications de taille et d'asymétrie de la couronne dentaire ont été suivies chez des individus portant les aneuploidies chromosomiques suivantes : syndrome de Down (DS), syndrome de Klinefelter (XXY), syndrome des hommes XYY et de Turner (XO). La taille des dents est généralement augmentée en présence d'un chromosome X ou Y additionnel, tandis que la perte d'un chromosome X résulte en une réduction de taille. L'effet le plus accentué de l'autosome supplémentaire dans le syndrome de Down consiste en une réduction de la taille des dents permanentes, mais quelques dents de lait sont plus grandes que la normale. Les fluctuations de l'asymétrie dentaire sont accrues dans les groupes XXY et DS, ce qui reflète une rupture de la stabilité du développement, mais ceci ne se manifeste pas dans le groupe XO.

Il apparaît que les deux chromosomes sexuels exercent une influence directe sur la taille dentaire en favorisant la croissance. Le chromosome Y semble affecter l'épaisseur de l'émail, peut-être en agissant sur l'amélogénèse, et aussi l'épaisseur de la dentine, peut-être en modifiant l'activité de prolifération cellulaire. Le rôle principal du chromosome X serait d'affecter le rythme de dépôt de l'émail. Les observations faites sur les dents dans le syndrome de Down concordent avec une réduction générale de l'activité mitotique des cellules dans cette condition. Les effets des aneuploidies chromosomiques sur la taille des dents ne sont pas uniformes à travers toute la denture, ce qui peut refléter des variations dans le taux et le rythme de la prolifération et de la différenciation cellulaires entre les germes dentaires en cours de développement.

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Introduction

Genetic influences on tooth crown size may be investigated in humans by studies of families, where associations between related individuals are quantified, or by studying individuals with chromosomal abnormalities, for example aneuploidies, where there may be loss or duplication of certain chromosomes.

Data from normal families have supported the concept of a polygenic basis to tooth-size variability, with phenotypic expression resulting from a combination of genetic and non-genetic (environmental) influences. It has been estimated that the heritability of tooth size, that is, the amount of variation due to additive genetic effects, is around 60 % for both deciduous and permanent dentitions (Townsend, 1980). The question of whether the sex chromosomes are involved in tooth-size variability has been controversial, some correlative studies indicating the existence of sex-linkage (Garn *et al.*, 1965; Lewis & Grainger, 1967), whilst others have not (Townsend & Brown, 1978; Potter *et al.*, 1983). However, most investigators have tested for evidence of X-linkage alone, and it is possible that the superimposed influence of the Y-chromosome may have complicated these analyses. In probably the only detailed study of both the sex chromosomes in normal individuals, Alvesalo (1971) analysed male and female cousin groups, as well as siblings, and found evidence that both X and Y chromosomes carry genes affecting tooth size, but the influence of the chromosomes on phenotypic expression appeared to differ.

Reports of tooth size in individuals with various chromosomal aneuploidies have indicated that autosomes and sex chromosomes both influence tooth size. The presence of an additional acrocentric autosome in Down syndrome leads to a marked reduction in permanent tooth size, although some of the deciduous teeth appear to be larger than normal (Barden, 1980; Townsend, 1983a). Extra or missing sex chromosomes also modify tooth size. For example, males with Klinefelter syndrome tend to have larger permanent teeth than normal, as do 47, XYY males, whereas permanent tooth size is reduced in Turner syndrome (Alvesalo *et al.*, 1975; Alvesalo and Kari, 1977; Kari *et al.*, 1980; Townsend & Alvesalo, 1985a, b; Townsend *et al.*, 1984). These results have suggested that both the X and Y chromosomes have growth-promoting roles.

Although teeth do not show any evidence of directional asymmetry in size, with one side being consistently larger than the other, small random differences are apparent between antimeric pairs (Townsend & Brown, 1980). Since genetic control is likely to be the same for corresponding teeth on both sides, the magnitude of these random differences, termed fluctuating asymmetry, should provide an indication of relative developmental stability within the dentition. One might expect therefore that fluctuating asymmetry would increase as the regulation of development, or so-called buffering ability, is reduced.

Shapiro (1975) proposed that there was a generalized decrease in developmental homeostasis in Down syndrome, which he referred to as amplified developmental instability, and this has recently been confirmed in a relatively large sample of Down syndrome individuals (Townsend, 1983b). However, to date little is known about the effects of altered sex chromosome complement on developmental stability within the dentition.

Human dental development commences around four weeks *in utero* with the formation of deciduous incisors, followed by the other deciduous and permanent teeth which each progress through a series of well-defined developmental stages. Final crown morphology is determined well before emergence and does not alter subsequently, apart from the effects of attrition, decay or restorative procedures. The dentition therefore provides a useful model system for the study of development from early in fetal life until adolescence. As more data accumulate relating to dental development in individuals with chromosomal abnormalities, we have an opportunity to undertake more detailed analyses of the patterns of tooth size and asymmetry in these conditions, giving consideration to both deciduous and permanent teeth and also comparing effects on different tooth dimensions and tooth groups.

Source : MNHN, Paris

A useful approach for displaying and comparing patterned deviations from normal within the dentition is the method of pattern profile analysis (Garn *et al.*, 1968; Garn *et al.*, 1984). In this study, profile patterns of crown size in both deciduous and permanent dentitions are presented for relatively large samples of individuals with chromosomal aneuploidies, namely Down syndrome (DS), Klinefelter (XXY) syndrome, XYY males and Turner (XO) syndrome. In addition, patterns of fluctuating dental asymmetry are presented for the different groups. We have attempted to improve understanding of the genetic influences on tooth size and to also provide some insight into the role of chromosomes on somatic growth and development in general.

Material and Method

Tooth-size measurements were recorded from dental casts of DS, XXY, XYY, XO and normal individuals obtained from collections in Australia, New Zealand, Finland, Denmark and the U.S.A. All subjects were of Caucasoid ancestry. Initial comparisons of mean tooth diameters and dental asymmetry showed no differences between the samples from different countries which were therefore combined for subsequent analysis. Study groups consisted of the following: 272 DS individuals, 199 males and 73 females; 77 XXY males, 21 XYY males and 121 XO females. The control group comprised 321 individuals, 150 males and 171 females, with no history of serious medical problems.

Mesiodistal and buccolingual tooth diameters of teeth on both sides of the dental arches were recorded by one investigator (G.T.) to an accuracy of 0.10 mm according to the definitions of Seipel (1946) and Moorrees *et al.* (1957) using specially modified dial calipers. Third molars, together with teeth which were not fully erupted or which showed evidence of attrition, were not included, nor were measurements attempted where caries, restorations, calculus or dental plaque obscured a dimension. Repeated determinations on separate occasions indicated that experimental errors were small, the standard deviation of a single determination (Dahlberg, 1940) averaging 0.08 mm.

As there were no statistically significant differences in mean values between sides, values averaged from right and left measurements were used in the analysis of crown size patterns. Measurements for individuals with chromosomal aneuploidies were converted into Z-scores against sex specific control groups according to the formula:

$$Z = (x - \bar{X})/SD$$

where x = raw measurement
$\bar{X}$ = control mean
SD = control standard deviation

Average Z-scores derived for each tooth dimension in the different study groups were then plotted to provide pattern profiles. Z-scores may be positive or negative, measurements above the control mean being associated with positive values, whereas measurements smaller than normal give negative scores. The magnitude of size reduction or increase for each study group was expressed as the mean Z-scores, averaged over all tooth dimensions, and also as the percentage variation in size compared with the control group. The degree of similarity in patterns between sexes, groups and dimensions was estimated by the correlation coefficient, r, computed from paired Z-scores of the two pattern profiles.

Fluctuating asymmetry was quantified by calculating V, the variance of the difference between sides adjusted for tooth size, i.e. variance of $(R - L)/(R + L)$ where R and L represent corresponding measurements on right and left sides respectively. Larger values of V are associated with greater asymmetry, smaller values with greater symmetry. The pattern of dental asymmetry in the different study groups was then determined where sample sizes permitted, and the degree of similarity in patterns quantified using the correlation coefficient, r, computed from paired values.

Results

A. *Crown size*

Down syndrome

Pattern profiles were initially constructed for males and females separately using sex specific controls. However, the patterns showed high

Source : MNHN, Paris

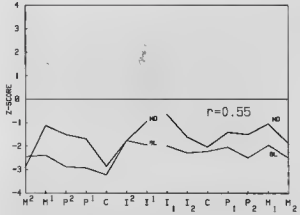

FIG. 1. — Crown size profile pattern for Down syndrome — mesiodistal and buccolingual dimensions of permanent teeth.

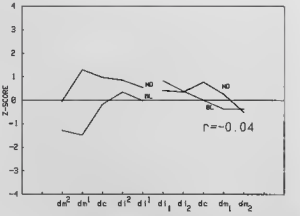

FIG. 2. — Crown size profile pattern for Down syndrome — mesiodistal and buccolingual dimensions of deciduous teeth.

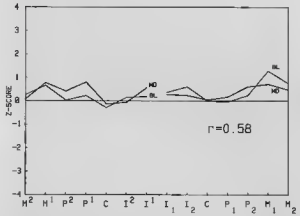

FIG. 3. — Crown size profile pattern for Klinefelter syndrome — mesiodistal and buccolingual dimensions of permanent teeth.

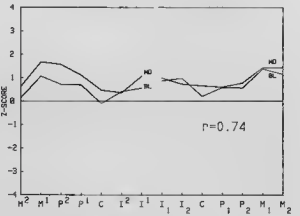

FIG. 4. — Crown size profile pattern for XYY males — mesiodistal and buccolingual dimensions of permanent teeth.

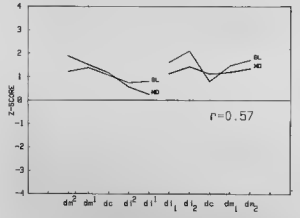

FIG. 5. — Crown size profile pattern for XYY males — mesiodistal and buccolingual dimensions of deciduous teeth.

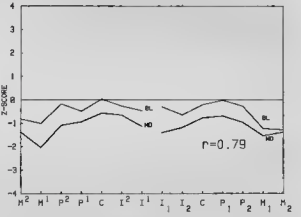

FIG. 6. — Crown size profile pattern for Turner syndrome — mesiodistal and buccolingual dimensions of permanent teeth.

Source : MNHN, Paris

concordance, r values being 0.92 for permanent tooth dimensions and 0.82 for deciduous tooth dimensions. Profiles are therefore presented using averaged values of the male and female Z-scores.

Permanent dentition (Fig. 1).

All tooth dimensions displayed negative Z-scores, indicating a generalized reduction in tooth size. Buccolingual dimensions showed a more marked deviation from normal than mesiodistal dimensions, average Z-scores being — 2.35 and — 1.55 respectively, corresponding with percentage reductions of 14.1 % and 9.0 % in tooth size. There was reasonable similarity in the patterns for mesiodistal and buccolingual dimensions, the value of r being 0.55. Central incisors and first molars showed least reduction in Z-scores whilst canines and second molars showed the largest negative values.

Deciduous dentition (Fig. 2).

Interestingly, many of the Z-scores were positive, indicating an increased tooth size compared with controls. Average Z-scores were 0.44 for mesiodistal dimensions and — 0.46 for buccolingual dimensions, corresponding to an average increase in size of 2.5 % and a reduction of 2.1 % respectively. For mesiodistal dimensions, only the second molars were associated with negative Z-scores, whereas the buccolingual dimensions of both deciduous molars provided negative Z-scores.

KLINEFELTER SYNDROME (47, XXY)

Insufficient data were available for analysis of the deciduous dentition, and so a profile pattern is presented for the permanent teeth only.

Permanent dentition (Fig. 3).

Most Z-scores were positive (24 out of 28) with average Z-scores being 0.30 for both mesiodistal and buccolingual dimensions. The average percentage increase in tooth size was 1.8 % for mesiodistal dimensions and 1.7 % for buccolingual. The patterns for these dimensions were similar, the value of r being 0.58. Canines tended to show lowest Z-scores (3 out of the 4 negative Z-values were associated with canine size), whilst first molars generally displayed high scores.

XYY MALES

Permanent dentition (Fig. 4).

All tooth dimensions were associated with positive Z-scores, except for the buccolingual dimension of the maxillary canine which scored slightly negatively. Average Z-scores were 0.91 for mesiodistal dimensions and 0.66 for buccolingual, the average percentage increases in size being 5.3 % and 3.9 % respectively. The similarity in patterns was good, r being 0.74. Generally, canine dimensions were associated with low Z-scores and first molar dimensions with high values.

Deciduous dentition (Fig. 5).

All dimensions were associated with positive Z-scores, average values being 1.23 for both mesiodistal and buccolingual dimensions. Average percentage increases in size were 6.4 % for mesiodistal dimensions and 6.8 % for buccolingual. The value of the pattern profile index, r, was 0.57.

TURNER SYNDROME (45, XO)

Permanent dentition (Fig. 6).

All tooth dimensions were associated with negative Z-scores, except for the buccolingual dimension of the maxillary canine, where Z = 0.03. Mesiodistal dimensions showed a greater deviation from normal than buccolingual dimensions, average Z-scores being — 1.08 and — 0.48 respectively, corresponding with percentage reductions of 6.1 % and 2.6 % in tooth size. The patterns of reduction were similar, r being 0.79. Generally, first molars showed high negative Z-scores whilst canines were associated with scores nearer to zero.

Deciduous dentition (Fig. 7).

Of the 20 dimensions, 9 were associated with positive Z-scores. Average Z-scores were — 0.50 for mesiodistal dimensions and — 0.15 for buccolingual dimensions, corresponding with average percentage reductions in tooth size of 2.6 % and 0.6 % respectively. The value of the index of pattern similarity, r, for the mesiodistal and buccolingual dimensions was 0.80. Dimensions

Source : MNHN, Paris

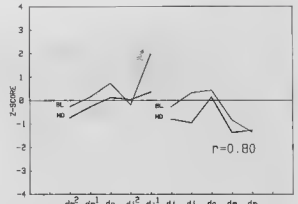

FIG. 7. — Crown size profile pattern for Turner syndrome — mesiodistal and buccolingual dimensions of deciduous teeth.

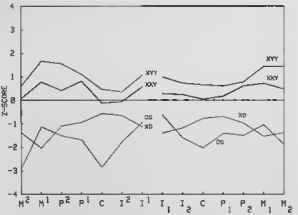

FIG. 8. — Comparison of crown size profile patterns in XYY, XXY, XO and DS groups — mesiodistal dimensions of permanent teeth.

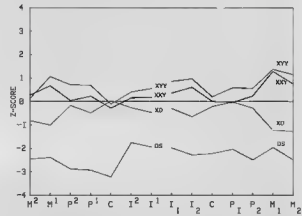

FIG. 9. — Comparison of crown size profile patterns in XYY, XXY, XO and DS groups — buccolingual dimensions of permanent teeth.

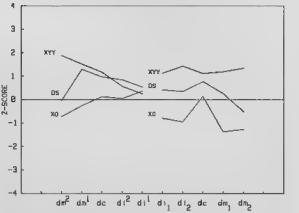

FIG. 10. — Comparison of crown size profile patterns in XYY, XO and DS groups — mesiodistal dimensions of deciduous teeth.

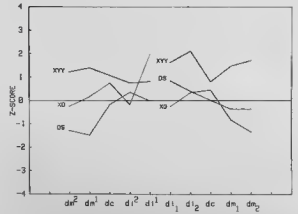

FIG. 11. — Comparison of crown size profile patterns in XYY, XO and DS groups — buccolingual dimensions of deciduous teeth.

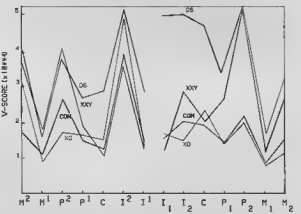

FIG. 12. — Fluctuating dental asymmetry in XXY, XO, DS and control groups — mesiodistal dimensions of permanent teeth.

Source : MNHN, Paris

of anterior teeth tended to be associated with positive scores whilst molars were associated with negative values.

Comparison of study groups

Figures 8, 9, 10 and 11 present comparisons of profile patterns for the different study groups. Values of r indicating similarity of pattern profiles are summarized in Tables 1 and 2, whilst mean Z-scores and average percentage variations in tooth size for each group compared with controls are given in Table 3.

Permanent dentition — mesiodistal dimensions (Fig. 8).

The general trend in Z-scores was as follows: XYY > XXY > XO > DS. In fact, there was no overlap of Z-values for the different dimensions between the four groups, except for central incisors and first molars in the XO and DS groups. XYY and XXY groups demonstrated similar pattern profiles, r being 0.79, and the DS group also showed some similarity in pattern to both XYY and XXY, r values being 0.51 and 0.59. However, the pattern for XO individuals was quite different from the other three groups, all r values being negative. When Z-values were compared between the groups for each dimension, the size of canines tended to show least deviation from normal for the groups with sex chromosomal aneuploidies, whereas the canine showed greatest deviation in the DS group. In contrast, the first molar was associated with large Z-values for XYY, XXY and XO groups, but not in the DS group.

Table 1. Indices of pattern similarity, r, for permanent tooth dimensions in chromosomal aneuploidies (md = mesiodistal, bl = buccolingual).

	DSmd	DSbl	XOmd	XObl	XXYmd	XXYbl	XYYmd	XYYbl
DSmd	—	0.55	— 0.40	— 0.14	0.59	0.43	0.51	0.70
DSbl		—	— 0.16	— 0.17	— 0.04	0.36	— 0.12	0.31
XOmd			—	0.79	— 0.61	— 0.75	— 0.75	— 0.68
XObl				—	— 0.53	— 0.89	— 0.60	— 0.69
XXYmd					—	0.58	0.79	0.70
XXYbl						—	0.58	0.86
XYYmd							—	0.74
XYYbl								—

Table 2. Indices of pattern similarity, r, for deciduous tooth dimensions in chromosomal aneuploidies (md = mesiodistal, bl = buccolingual).

	DSmd	DSbl	XOmd	XObl	XXYmd	XYYbl
DSmd	—	— 0.04	0.70	0.54	— 0.27	— 0.45
DSbl		—	0.06	0.13	— 0.54	0.06
XOmd			—	0.80	— 0.57	— 0.81
XObl				—	— 0.53	— 0.47
XYYmd					—	0.57
XYYbl						—

Table 3. Average Z-scores for tooth crown size in chromosomal aneuploidies.

	Deciduous		Permanent	
Syndrome	md	bl	md	bl
DS	0.44 (+ 2.5 %)	— 0.46 (— 2.1 %)	— 1.55 (— 9.0 %)	— 2.35 (— 14.1 %)
XO	— 0.50 (— 2.6 %)	— 0.15 (— 0.6 %)	— 1.08 (— 6.1 %)	— 0.48 (— 2.6 %)
XXY	—	—	0.30 (+ 1.8 %)	0.30 (+ 1.7 %)
XYY	1.23 (+ 6.4 %)	1.23 (+ 6.8 %)	0.91 (+ 5.3 %)	0.66 (+ 3.9 %)

% variation given in parentheses.

Source : MNHN, Paris

Permanent dentition — buccolingual dimensions (Fig. 9).

The different study groups showed similar trends in Z-scores for buccolingual dimensions as they did for mesiodistal. The XYY groups consistently demonstrated high Z-scores, whilst the DS group was associated with low scores. Pattern profiles for the XYY and XXY groups were similar ($r = 0.86$), whilst the XO group showed least similarity in patterning with the other groups. Again, canines displayed least variation from normal size and first molars greatest variation in the three groups with sex chromosomal aneuploidy. This trend was reversed in the DS group.

Deciduous — mesiodistal dimensions (Fig. 10).

The trend in Z-scores was generally as follows: XYY > DS > XO, although maxillary incisors showed highest scores in the DS group. The DS and XO groups had similar patterns ($r = 0.70$), whereas both of these groups showed quite different patterns to the XYY group ($r = -0.27$ and -0.57 respectively).

Deciduous — buccolingual dimensions (Fig. 11).

Scores for the XYY group were generally highest, whilst the DS and XO groups showed some overlap in values, Z-scores tending to be higher in the XO group for maxillary dimensions, but lower for mandibular dimensions. The plots showed little similarity in their patterns, values of r ranging from 0.13 between DS and XO groups to -0.47 between XYY and XO groups.

B. *Dental asymmetry*

Permanent dentition.

Fig. 12 and 13 compare patterns of asymmetry in the permanent dentition between the different groups for mesiodistal and buccolingual dimensions. Initial statistical testing failed to show any evidence of directional asymmetry in any of the groups, nor were any significant differences noted in dental asymmetry between males and females. Analyses were therefore performed for both sexes combined in these groups. The XYY group was not included in any of the asymmetry analyses due to insufficient numbers being available.

Values for asymmetry were lowest in the control and XO groups, none of the values of V differing significantly between these two groups. The XXY group showed a tendency for increased asymmetry, 18 of a possible 28 comparisons giving larger V values than controls, 5 being significant at $p < 0.05$. The DS group showed a marked increase in asymmetry, values for all dimensions being significantly greater than in controls.

The general pattern of asymmetry values was similar in all four groups. Maxillary lateral incisors showed greatest asymmetry for both mesiodistal and buccolingual dimensions, whilst first molars showed least asymmetry. Generally the distal tooth in each tooth class, *i.e.* lateral incisors, second premolars and second molars, tended to show greater asymmetry than the more mesial teeth. When r values were determined to compare patterns of asymmetry, values were generally high ranging from 0.31 between XO and XXY groups for mesiodistal dimensions, to 0.93 between DS and XO groups for buccolingual dimensions.

Deciduous dentition.

Figs. 14 and 15 provide variance data for control and DS groups. Data for other groups are not presented in graphical form as the sample sizes were small. However, for those dimensions in the XO group where the sample size exceeded 15, no evidence of increased asymmetry was noted compared with normal. For 19 of the 20 comparisons, the DS group showed larger asymmetry values than the control group, with 9 differences being statistically significant at $p < 0.05$. The general pattern of values was similar in both groups, with $r = 0.37$ for mesiodistal dimensions and $r = 0.92$ for buccolingual dimensions. For both dimensions, the second molar tended to show least asymmetry whereas the buccolingual dimensions of mandibular incisors showed high values.

Source : MNHN, Paris

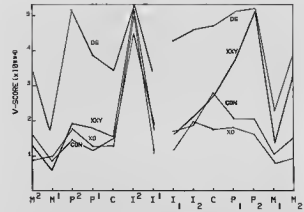

FIG. 13. — Fluctuating dental asymmetry in XXY, XO, DS and control groups — buccolingual dimensions of permanent teeth.

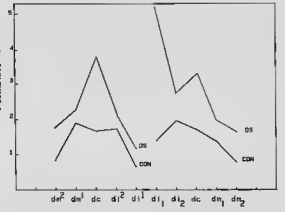

FIG. 14. — Fluctuating dental asymmetry in DS and control groups — mesiodistal dimensions of deciduous teeth.

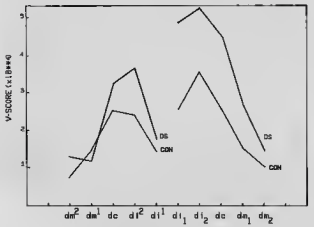

FIG. 15. — Fluctuating dental asymmetry in DS and control groups — buccolingual dimensions of deciduous teeth.

DISCUSSION

The final size of dental crowns reflects the timing of onset and rate of proliferation and differentiation of the inner enamel epithelium of the developing tooth germ together with deposition of mineralized tissue (Keene, 1982). The shape of eacb crown is basically established once the spread of dentinal mineralization has extended across the region of the future dentino-enamel junction. Subsequent modifications of size or shape result from variations in the thickness of enamel deposition over the crown.

Abberations in chromosomal number, whether they involve the sex chromosomes or an autosome are associated with altered tooth size. Extra X and Y cbromosomes lead to an increase in tooth size, wbereas the loss of an X chromosome or an additional chromosome 21 result in reduced permanent tooth size. Although some minor variations in crown shape have also been noted in individuals with sex chromosome abnormalities (e.g. by Townsend *et al.*, 1984), the autosomal imbalance in Down syndrome causes more severe morphological crown abnormalities. Nevertheless, in all the instances of chromosomal aneuploidy which we have reported, the effects on tooth size do not appear to be uniform. Rather, responses differ between deciduous and permanent dentitions, between mesiodistal and buccolingual dimensions, and also between different teeth or tooth groups.

When the crown size profile patterns for the DS group are considered, we find that the permanent teeth are considerably reduced in size,

Source : MNHN, Paris

but some of the deciduous teeth, especially anterior teeth, are in fact larger than normal. The observed reduction in permanent tooth size is in agreement with the reports of others including Kisling (1966), Geciauskas & Cohen (1970) and Prahl-Andersen & Oerlemans (1976). Furthermore, greater reduction was noted in the later-forming teeth, i.e. lateral incisors, canines and second molars, compared with those that form earlier, i.e. central incisors and first molars. This finding, together with the tendency for later-forming components of teeth and later-determined dental dimensions to be more affected (Townsend, 1983a), lends support to the theory that the chromosomal imbalance in Down syndrome leads to a decrease in cellular mitotic activity.

The results for deciduous teeth were surprising, but support the independent findings of Alexandersen (1969) and also Barden (1980). There may be an initial transitory acceleration in cellular activity at about the 8-10th week *in utero*, as suggested by Barden (1980), which could persist during the initial stages of mineralization. This acceleration may then be followed by the retardation of growth which becomes evident in permanent tooth dimensions. However, the result may be due to a sampling effect, as the dentitions examined represent only those DS individuals who have survived to reach childhood or early adulthood. The rate of spontaneous abortion in DS is high (Creasy & Crolla, 1974), and so the subjects whom we have studied are amongst the fitter individuals; that is, at the fitter end of a spectrum. If cellular activity during the critical prenatal stage is related to survival, then those fetuses who have experienced severe growth disturbance prenatally may have been aborted, leaving those who have suffered little, if any, growth retardation. This effect would presumably be reflected in the size of those teeth which were forming at that critical time, namely the deciduous anterior teeth.

Both deciduous and permanent teeth were larger in XYY males and permanent teeth were also larger in XXY males, lending support to the idea that the X and Y chromosomes have some direct chromosomal effect on growth. Whilst an hormonal effect cannot be ruled out, there is no evidence that hormonal levels are abnormal in XXY and XYY males; in fact both plasma testosterone and urinary androgen secretion seem normal in XYY males (Polani, 1972). Indeed, whatever influences lead to the increase in tooth size in these groups, they must operate from very early on during development; for example, the deciduous teeth begin to form before or at about the time when the gonads differentiate. Furthermore, it appears that the larger tooth size in 47, XYY males results from an increase in both enamel and dentine thickness (Alvesalo & Tammisalo, 1985).

Alvesalo & Varrela (1980) have shown that individuals with complete testicular feminization syndrome (46, XY), where target organs fail to react to androgens, have teeth as large as normal males. This also suggests that the Y chromosome has a direct effect on dental development. Also, Tanner *et al.*, (1959) in their study of skeletal development in XXY, XO and normal individuals, found that the rate of skeletal maturation in XXY individuals and normal XY males was delayed compared with the rate of both XO and XX females. The Y chromosome therefore produced retardation whether one or two X chromosomes were present but, without the Y, neither one or two X chromosomes produced an effect. Tanner and his colleagues concluded that genes on the Y chromosome produced the normal differences in rate of development between the sexes and they favoured the concept of a direct chromosomal effect rather than an hormonal influence because androgens normally cause an acceleration in maturation, not a delay.

Our findings in the deciduous dentition of the XO group may reflect a similar sampling effect to that discussed for the DS group. Indeed, the rate of spontaneous abortion in Turner syndrome has been estimated to be about 97-99 % (Polani, 1981). Obviously only survivors have been examined, presumably those whose cellular activity was not severely disrupted during the critical prenatal period when the deciduous anterior teeth were forming.

The tendency for mesiodistal dimensions to show greater reduction in size than the buccolingual in the XO group may be the result of a decrease in enamel thickness in Turner syndrome. Alvesalo & Tammisalo (1981) confirmed in a radiographic study that the enamel layer in incisor and canine teeth of XO females was significantly reduced compared with normal controls. However, the distance between the mesial and distal dentino-enamel junctions, which

Source : MNHN, Paris

reflects dentinal thickness, was not reduced. Enamel is generally thicker across the maximum mesiodistal dimension of teeth (Shillingburg & Grace, 1973), so a uniform percentage decrease in enamel thickness would be likely to produce a greater reduction in mesiodistal crown diameter than buccolingual. It is also worth pointing out that no significant differences were noted in enamel thickness between normal males and females in this study, the larger average size of teeth in males being due to thicker dentine. It would seem therefore, that a second sex chromosome, whether X or Y leads to an increase in enamel thickness, whereas the Y chromosome appears to also influence dentine thickness.

Of all the permanent teeth studied in the three groups with sex chromosomal aneuploidies, the canine seems to be the least affected tooth, whereas the first molar shows greatest deviation from normal. This becomes more interesting when we consider the normal pattern of sexual dimorphism in males and females, where the canine tends to show greater sexual dimorphism than other teeth. It has been suggested that the canine tends to be developmentally and genetically independent of the other teeth (Alvesalo *et al.*, 1975) and in odontometric studies of normal populations it does tend to be quite stable in size. However, if the development of these teeth is taken into account, the first molar forms earlier and over a shorter time than the canine. If we postulate that both direct genetic effects and superimposed hormonal influences contribute to final phenotype, perhaps the canines normally reach their maximum size potential; that is, their genetic potential is fully realized, and therefore additional sex chromosomes may have little effect on their size. On the other hand, earlier-forming teeth may still retain some potential for additional growth under certain circumstances, for example, under the influence of an additional sex chromosome.

When fluctuating asymmetry patterns are considered, it appears that autosomal aneuploidy produces a greater disruption to developmental homeostasis than addition or loss of sex chromosomes. The DS group showed significantly elevated dental asymmetry in both dentitions, confirming the hypothesis of Shapiro (1975) that this condition leads to a decrease in developmental stability. There was some suggestion that asymmetry was elevated in the XXY group compared with controls but no effect was noticeable in the XO group. It should be noted, as Holly Smith *et al.*, (1982) have stressed, that problems exist in relation to statistical power and sample size in all human studies of dental asymmetry. The large DS sample available has enabled reasonably firm conclusions to be drawn for this group but still larger samples are needed for the groups with sex chromosomal abnormalities.

The general patterns of asymmetry were similar in all groups, with the more distal tooth in each group tending to show greater asymmetry than the more mesial members. Both the permanent canine and first permanent molar displayed relatively little asymmetry compared with other teeth.

In DS individuals there is evidence that the additional chromosomal material decreases the mitotic activity of cells by increasing the length of the G2 phase of mitosis (Paton *et al.*, 1974). In regard to the sex chromosomes, Barlow (1973) has shown that additional X and Y chromosomes may influence phenotypic characters such as fingerprints, stature, IQ and birth weight in a regular manner. Since the Y chromosome and each X chromosome in excess of one are largely heterochromatic, Barlow has suggested that this phenotypic effect results from the influence of total heterochromatic load on cellular mitotic activity. Cavalier-Smith (1978) has provided cogent arguments to support the concept that heterochromatin acts as an important regulator of nuclear volume and cell division.

Tooth size appears to be a polygenic autosomal trait which is influenced by the sex chromosomes complement, whether normal or abnormal. The X and Y chromosomes both seem to have a similar influence on enamel thickness, possibly by regulating amelogenesis, whereas the Y chromosome appears to have a greater effect on dentine thickness, perhaps by modifying cellular proliferative activity. This differential effect could explain the observed differences in tooth size between normal males and females. The autosomal imbalance in Down syndrome seems to produce a reduction in cellular activity of developing tooth germs. Furthermore, the different responses of teeth throughout the dentition to chromosomal aneuploidies is likely to reflect variations in timing and rate of cell proliferation and differentiation between developing tooth germs.

Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

APPENDIX

This appendix contains tabulated data from which the figures were produced.

Z-scores for crown size in the permanent dentition of individuals with Down syndrome (male and female scores combined)

Tooth	n	Z-score	Tooth	n	Z-score
Mesiodistal			**Buccolingual**		
	MAXILLA			MAXILLA	
I1	212	−0.94	I1	107	−1.94
I2	138	−1.76	I2	69	−1.75
C	136	−2.86	C	92	−3.22
P1	174	−1.69	P1	162	−2.93
P2	142	−1.51	P2	136	−2.88
M1	207	−1.12	M1	212	−2.38
M2	127	−2.90	M2	124	−2.45
	MANDIBLE			MANDIBLE	
I1	184	−0.64	I1	118	−1.98
I2	189	−1.61	I2	116	−2.28
C	175	−2.03	C	140	−2.21
P1	178	−1.40	P1	171	−2.03
P2	148	−1.50	P2	144	−2.49
M1	195	−1.03	M1	206	−1.95
M2	91	−1.88	M2	103	−2.49
Weighted average		−1.55	Weighted average		−2.35

Source : MNHN, Paris

Crown size in the permanent dentition of individuals with Down syndrome

Tooth	Males n	Males $\bar{x}$	Males Z-score	Males %	Females n	Females $\bar{x}$	Females Z-score	Females %
Mesiodistal								
			MAXILLA					
I1	157	8.31	— 0.86	— 5.1	55	7.97	— 1.16	— 7.4
I2	106	5.93	— 1.68	— 13.4	32	5.58	— 2.02	— 16.6
C	107	6.86	— 2.75	— 14.7	29	6.59	— 3.26	— 14.7
P1	128	6.41	— 1.68	— 9.3	46	6.31	— 1.73	— 9.5
P2	109	6.16	— 1.38	— 9.0	33	5.96	— 1.93	— 9.8
M1	150	10.11	— 1.08	— 5.1	57	9.78	— 1.22	— 5.5
M2	97	8.62	— 2.96	— 16.4	30	8.35	— 2.69	— 16.2
			MANDIBLE					
I1	137	5.28	— 0.59	— 3.5	47	5.17	— 0.77	— 4.4
I2	140	5.49	— 1.56	— 9.1	49	5.33	— 1.74	— 10.7
C	128	6.22	— 1.92	— 11.0	47	5.89	— 2.33	— 11.6
P1	130	6.59	— 1.31	— 8.3	48	6.40	— 1.64	— 9.3
P2	106	6.60	— 1.50	— 9.5	42	6.46	— 1.49	— 8.1
M1	145	10.78	— 1.09	— 5.6	50	10.42	— 0.86	— 4.9
M2	72	9.75	— 1.82	— 10.9	19	9.12	— 2.12	— 12.8
Weighted average			— 1.51	— 8.9			— 1.66	— 9.4
Buccolingual								
			MAXILLA					
I1	83	6.32	— 1.96	— 13.9	24	6.28	— 1.89	— 12.2
I2	60	5.60	— 1.71	— 14.8	9	5.37	— 2.05	— 16.0
C	71	6.92	— 3.10	— 19.7	21	6.56	— 3.63	— 19.9
P1	120	7.86	— 2.89	— 17.0	42	7.72	— 3.03	— 16.2
P2	106	7.79	— 2.84	— 18.0	30	7.57	— 3.01	— 17.7
M1	153	10.47	— 2.35	— 11.0	59	10.19	— 2.45	— 10.7
M2	95	10.15	— 2.31	— 14.1	29	9.59	— 2.89	— 16.0
			MANDIBLE					
I1	90	5.27	— 2.02	— 14.7	28	5.21	— 1.86	— 13.0
I2	88	5.49	— 2.27	— 14.8	28	5.38	— 2.30	— 14.9
C	106	6.76	— 2.19	— 14.6	34	6.36	— 2.29	— 15.5
P1	128	6.98	— 2.13	— 14.1	43	6.87	— 1.75	— 12.0
P2	103	7.27	— 2.58	— 15.9	41	7.19	— 2.28	— 14.4
M1	151	9.82	— 2.06	— 9.3	55	9.72	— 1.66	— 7.4
M2	83	9.26	— 2.44	— 13.6	20	8.87	— 2.68	— 14.2
Weighted average			— 2.35	— 14.3			— 2.36	— 13.5

Source : MNHN, Paris

Crown size in the deciduous dentition of individuals with Down syndrome

Tooth	Males n	Males $\bar{x}$	Males Z-score	Males %	Females n	Females $\bar{x}$	Females Z-score	Females %
Mesiodistal								
				MAXILLA				
di1	21	6.68	0.45	3.1	8	6.63	0.74	3.9
di2	31	5.50	0.84	5.2	14	5.44	0.85	4.8
dc	75	7.14	0.81	3.8	27	7.21	1.38	7.0
dm1	56	7.64	1.29	7.5	24	7.55	1.30	8.0
dm2	74	8.91	— 0.07	— 0.3	33	8.81	0.00	0.0
				MANDIBLE				
di1	17	4.22	0.72	5.5	8	3.92	— 0.24	— 1.8
di2	21	4.74	0.46	3.7	12	4.67	0.13	0.9
dc	52	6.08	0.67	3.6	14	5.99	1.15	5.3
dm1	55	7.96	0.30	1.5	22	7.74	0.14	0.7
dm2	69	9.78	— 0.51	— 2.4	28	9.56	— 0.51	— 2.6
Weighted average			0.43	2.5			0.48	2.6
Buccolingual								
				MAXILLA				
di1	20	4.99	0.13	0.8	8	4.81	— 0.43	— 2.4
di2	32	4.95	0.33	2.7	14	4.86	0.40	3.0
dc	69	6.12	— 0.33	— 1.9	26	6.15	0.20	1.3
dm1	59	8.11	— 1.67	— 7.9	24	8.05	— 1.04	— 5.2
dm2	76	9.39	— 1.48	— 6.5	34	9.35	— 0.88	— 4.1
				MANDIBLE				
di1	15	3.88	0.51	4.0	7	4.06	1.50	10.0
di2	22	4.34	0.37	1.9	10	4.39	0.41	2.3
dc	49	5.67	— 0.08	— 0.4	15	5.65	0.27	1.6
dm1	53	7.17	— 0.42	— 2.4	21	7.11	— 0.27	— 1.5
dm2	75	8.68	— 0.41	— 2.3	31	8.61	— 0.26	— 1.3
Weighted average			— 0.56	— 2.6			— 0.22	— 0.9

Source : MNHN, Paris

Z-scores for crown size in the deciduous dentition of individuals with Down syndrome (male and female scores combined)

Tooth	n	Z-score	Tooth	n	Z-score
Mesiodistal			**Buccolingual**		
	MAXILLA			MAXILLA	
di1	29	0.53	di1	28	— 0.03
di2	45	0.84	di2	46	0.35
dc	102	0.96	dc	95	— 0.18
dm1	80	1.29	dm1	83	— 1.49
dm2	107	— 0.05	dm2	110	— 1.29
	MANDIBLE			MANDIBLE	
di1	25	0.41	di1	22	0.83
di2	33	0.34	di2	32	0.38
dc	66	0.77	dc	64	0.00
dm1	77	0.25	dm1	74	— 0.38
dm2	97	— 0.51	dm2	106	— 0.37
Weighted average		0.44	Weighted average		— 0.46

Crown size in the permanent dentition of XXY males

Tooth	n	$\bar{x}$	Z-score	%	Tooth	n	$\bar{x}$	Z-score	%
Mesiodistal					**Buccolingual**				
		MAXILLA					MAXILLA		
I1	51	9.06	0.57	3.4	I1	44	7.43	0.18	1.2
I2	44	6.82	— 0.06	— 0.4	I2	33	6.66	0.16	1.4
C	48	7.99	— 0.13	— 0.6	C	42	8.46	— 0.29	— 1.9
P1	40	7.39	0.81	4.5	P1	48	9.60	0.23	1.4
P2	31	6.95	0.41	2.7	P2	43	9.52	0.03	0.2
M1	27	11.04	0.78	3.7	M1	48	12.13	0.67	3.1
M2	29	10.35	0.07	0.4	M2	40	12.01	0.27	1.7
		MANDIBLE					MANDIBLE		
I1	55	5.56	0.28	1.6	I1	41	6.35	0.37	2.8
I2	60	6.12	0.23	1.3	I2	44	6.70	0.61	4.0
C	64	7.01	0.04	0.3	C	50	7.92	0.00	0.0
P1	56	7.27	0.17	1.1	P1	56	8.11	— 0.04	— 0.2
P2	33	7.57	0.61	3.8	P2	37	8.77	0.24	1.5
M1	24	11.84	0.72	3.7	M1	41	11.46	1.29	5.8
M2	23	11.25	0.47	2.8	M2	30	11.17	0.75	4.2
Weighted average			0.30	1.8	Weighted average			0.30	1.7

Source : MNHN, Paris

Crown size in the permanent dentition of XYY males

Tooth	n	x̄	Z-score	%	Tooth	n	x̄	Z-score	%
Mesiodistal					**Buccolingual**				
		MAXILLA					MAXILLA		
I1	18	9.33	1.07	6.5	I1	15	7.63	0.56	4.0
I2	18	7.04	0.35	2.8	I2	12	6.80	0.41	3.5
C	14	8.24	0.46	2.5	C	12	8.56	— 0.11	— 0.7
P1	13	7.50	1.10	6.1	P1	15	9.85	0.69	4.0
P2	11	7.46	1.56	10.2	P2	14	9.93	0.71	4.5
M1	10	11.49	1.67	7.9	M1	12	12.35	1.07	5.0
M2	5	10.66	0.61	3.4	M2	4	11.90	0.13	0.8
		MANDIBLE					MANDIBLE		
I1	14	5.79	0.99	5.9	I1	9	6.57	0.87	6.3
I2	16	6.29	0.72	4.1	I2	9	6.85	0.98	6.4
C	16	7.25	0.65	3.7	C	11	8.03	0.20	1.4
P1	10	7.47	0.60	3.9	P1	12	8.45	0.59	3.9
P2	8	7.65	0.78	4.9	P2	11	8.94	0.56	3.5
M1	12	12.27	1.44	7.4	M1	13	11.50	1.38	6.2
M2	3	11.87	1.43	8.5	M2	5	11.41	1.15	6.4
Weighted average			0.91	5.3	Weighted average			0.66	3.9

Crown size in the deciduous dentition of XYY males

Tooth	n	x̄	Z-score	%	Tooth	n	x̄	Z-score	%
Mesiodistal					**Buccolingual**				
		MAXILLA					MAXILLA		
di1	3	6.58	0.24	1.5	di1	3	5.18	0.81	4.6
di2	5	5.41	0.56	3.4	di2	5	5.11	0.74	6.0
dc	7	7.25	1.16	5.4	dc	9	6.63	1.06	6.3
dm1	5	7.73	1.51	8.7	dm1	8	9.39	1.39	6.6
dm2	8	9.69	1.88	8.4	dm2	8	10.58	1.22	5.4
		MANDIBLE					MANDIBLE		
di1	1	4.35	1.13	8.8	di1	2	4.20	1.62	12.6
di2	2	5.10	1.43	11.6	di2	2	4.73	2.11	11.0
dc	6	6.23	1.11	6.1	dc	6	5.93	0.79	4.2
dm1	3	8.32	1.19	6.1	dm1	6	7.98	1.47	8.6
dm2	5	10.65	1.34	6.3	dm2	6	9.70	1.71	9.2
Weighted average			1.23	6.4	Weighted average			1.23	6.8

Source : MNHN, Paris

Crown size in the permanent dentition of XO females

Tooth	n	$\bar{x}$	Z-score	%	Tooth	n	$\bar{x}$	Z-score	%
Mesiodistal					**Buccolingual**				
		MAXILLA					MAXILLA		
I1	109	7.98	— 1.14	—7.3	I1	82	6.93	— 0.47	—3.1
I2	112	6.33	— 0.66	—5.4	I2	79	6.26	— 0.27	—2.0
C	110	7.53	— 0.57	—2.6	C	91	8.21	0.03	0.2
P1	103	6.61	— 0.94	—5.2	P1	101	8.97	— 0.49	—2.6
P2	98	6.24	— 1.09	—5.6	P2	102	9.11	— 0.17	—1.0
M1	93	9.39	— 2.04	—9.3	M1	102	10.91	— 1.01	—4.4
M2	46	9.13	— 1.38	—8.3	M2	58	10.90	— 0.82	—4.5
		MANDIBLE					MANDIBLE		
I1	103	4.98	— 1.40	—7.9	I1	80	5.86	— 0.30	—2.2
I2	110	5.54	— 1.18	—7.2	I2	89	6.05	— 0.65	—4.3
C	112	6.40	— 0.77	—3.9	C	92	7.42	— 0.21	—1.5
P1	111	6.79	— 0.69	—3.8	P1	105	7.80	— 0.02	—0.1
P2	103	6.66	— 0.97	—5.3	P2	107	8.25	— 0.28	—1.8
M1	86	9.59	— 1.54	—8.9	M1	94	9.92	— 1.23	—5.5
M2	46	9.59	— 1.38	—8.3	M2	55	9.63	— 1.28	—6.9
Weighted average			— 1.08	—6.1	Weighted average			— 0.48	—2.6

Crown size in the deciduous dentition of XO females

Tooth	n	$\bar{x}$	Z-score	%	Tooth	n	$\bar{x}$	Z-score	%
Mesiodistal					**Buccolingual**				
		MAXILLA					MAXILLA		
di1	5	6.50	0.36	1.9	di1	1	5.50	1.97	11.6
di2	9	5.20	0.03	0.2	di2	5	4.65	— 0.19	—1.5
dc	20	6.78	0.12	0.6	dc	17	6.37	0.74	4.9
dm1	19	6.87	— 0.27	—1.7	dm1	19	8.55	0.15	0.7
dm2	23	8.46	— 0.74	—4.0	dm2	23	9.64	— 0.26	—1.1
		MANDIBLE					MANDIBLE		
di1	3	3.75	— 0.80	—6.0	di1	2	3.63	— 0.26	—1.6
di2	5	4.36	— 0.96	—5.8	di2	3	4.37	0.33	1.9
dc	19	5.73	0.14	0.7	dc	13	5.70	0.44	2.5
dm1	17	7.19	— 1.38	—6.5	dm1	14	6.88	— 0.84	—4.7
dm2	18	9.19	— 1.27	—6.4	dm2	16	8.14	— 1.36	—6.7
Weighted average			— 0.50	—2.6	Weighted average			— 0.15	—0.6

Source : MNHN, Paris

Fluctuating asymmetry in the permanent dentition of control, XO, XXY and Down syndrome groups

Tooth	Controls N	Controls V (× 10⁴)	XO N	XO V (× 10⁴)	XXY N	XXY V (× 10⁴)	DS N	DS V (× 10⁴)	Tooth	Controls N	Controls V (× 10⁴)	XO N	XO V (× 10⁴)	XXY N	XXY V (× 10⁴)	DS N	DS V (× 10⁴)
Mesiodistal									**Buccolingual**								
				MAXILLA									MAXILLA				
I1	218	1.44	105	1.29	42	1.20	178	2.74**	I1	157	1.67	80	1.06	41	1.56	88	3.44**
I2	196	3.99	98	4.93	35	3.54	90	8.16**	I2	128	4.43	65	5.07	32	4.99	43	10.48**
C	149	1.28	105	1.55	45	1.16	99	2.94**	C	145	1.48	84	1.29	38	1.47	60	3.36**
P1	127	1.57	90	1.72	25	1.91	141	2.72**	P1	144	1.14	93	1.24	41	1.77	134	3.79**
P2	126	2.71	85	1.76	14	4.10	102	3.81*	P2	149	1.45	94	1.75	29	1.86	103	5.85**
M1	145	1.13	73	0.95	10	1.77	176	1.73**	M1	209	0.85	95	0.94	33	0.62	191	1.74**
M2	85	1.74	32	3.13	11	3.64	103	4.06**	M2	109	1.54	41	0.86	25	1.25	91	3.33**
				MANDIBLE									MANDIBLE				
I1	211	1.59	99	1.71	48	1.20	157	5.51**	I1	155	1.68	74	1.16	40	1.62	98	4.24**
I2	214	2.07	102	1.58	52	2.88	151	5.62**	I2	152	1.82	80	1.95	38	2.06	96	4.52**
C	169	1.93	109	2.40	58	2.04	152	4.73**	C	129	2.76	79	1.71	36	2.68	103	4.63*
P1	144	1.47	99	1.43	38	2.67*	150	3.41**	P1	147	2.02	99	1.79	43	3.72*	147	5.36**
P2	131	2.21	88	2.05	18	8.95**	116	5.63**	P2	144	2.02	97	1.55	26	5.80**	113	5.88**
M1	119	0.82	55	0.86	9	1.12	165	1.57**	M1	183	1.04	73	0.76	22	1.36	178	2.25**
M2	79	1.53	24	1.20	9	2.69	47	3.29**	M2	97	1.48	34	0.88	20	3.23*	65	3.77**

* Significantly different from control at $p < 0.05$.
** Significantly different from control at $p < 0.01$.

Fluctuating asymmetry in the deciduous dentition of control, XO and Down syndrome groups

Tooth	Controls N	Controls V (× 10⁴)	XO N	XO V (× 10⁴)	DS N	DS V (× 10⁴)	Tooth	Controls N	Controls V (× 10⁴)	XO N	XO V (× 10⁴)	DS N	DS V (× 10⁴)
Mesiodistal							**Buccolingual**						
				MAXILLA							MAXILLA		
di1	48	0.66	5	1.02	25	1.12	di1	52	1.43	2	0.00	23	1.72
di2	77	1.73	8	2.46	35	2.09	di2	72	2.41	3	1.18	37	3.61
dc	123	1.70	17	1.74	75	3.77**	dc	121	2.51	13	2.53	72	3.23
dm1	88	1.89	15	0.81	62	2.23	dm1	98	1.48	14	0.52	66	1.19
dm2	94	0.83	17	0.63	84	1.73**	dm2	118	0.78	20	0.36	93	1.30**
				MANDIBLE							MANDIBLE		
di1	36	1.40	3	2.05	22	6.44**	di1	35	2.57	2	8.45	18	4.81
di2	59	1.97	4	26.33	26	2.69	di2	59	3.51	3	2.94	28	8.48**
dc	111	1.71	16	1.91	49	3.24*	dc	107	2.54	12	3.14	44	4.43*
dm1	79	1.39	10	17.20	57	1.93	dm1	105	1.51	10	1.95	65	2.66**
dm2	88	0.79	13	11.00	79	1.60**	dm2	106	1.05	10	0.95	90	1.45

* Significantly different from control at $p < 0.05$.
** Significantly different from control at $p < 0.01$.

Source : MNHN, Paris

Crown size in the deciduous dentition of normal individuals

	Males			Females				Males			Females		
Tooth	n	$\bar{x}$	SD	n	$\bar{x}$	SD	Tooth	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Mesiodistal							**Buccolingual**						
		MAXILLA								MAXILLA			
di1	27	6.48	0.44	35	6.38	0.33	di1	30	4.95	0.29	36	4.93	0.29
di2	42	5.23	0.32	43	5.19	0.29	di2	42	4.82	0.39	41	4.72	0.36
dc	54	6.88	0.32	74	6.74	0.34	dc	54	6.24	0.37	72	6.07	0.40
dm1	40	7.11	0.41	63	6.99	0.43	dm1	48	8.81	0.42	69	8.49	0.42
dm2	42	8.94	0.40	76	8.81	0.47	dm2	50	10.04	0.44	78	9.75	0.45
		MANDIBLE								MANDIBLE			
di1	17	4.00	0.31	24	3.99	0.30	di1	16	3.73	0.29	22	3.69	0.25
di2	36	4.57	0.37	37	4.63	0.28	di2	34	4.26	0.22	35	4.29	0.23
dc	53	5.87	0.32	66	5.69	0.26	dc	51	5.69	0.31	65	5.56	0.32
dm1	43	7.84	0.40	60	7.69	0.36	dm1	49	7.35	0.43	65	7.22	0.41
dm2	43	10.02	0.47	65	9.82	0.50	dm2	48	8.88	0.48	72	8.72	0.43

Crown size in the permanent dentition of normal individuals

	Males			Females				Males			Females		
Tooth	n	$\bar{x}$	SD	n	$\bar{x}$	SD	Tooth	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Mesiodistal							**Buccolingual**						
		MAXILLA								MAXILLA			
I1	104	8.76	0.53	125	8.61	0.55	I1	81	7.34	0.52	85	7.15	0.46
I2	95	6.85	0.55	111	6.69	0.55	I2	71	6.57	0.57	77	6.39	0.50
C	82	8.04	0.43	81	7.73	0.35	C	81	8.62	0.55	78	8.19	0.45
P1	74	7.07	0.39	77	6.97	0.38	P1	76	9.47	0.56	81	9.21	0.49
P2	74	6.77	0.44	77	6.61	0.34	P2	83	9.50	0.60	82	9.20	0.54
M1	81	10.65	0.50	107	10.35	0.47	M1	98	11.76	0.55	121	11.41	0.50
M2	65	10.31	0.57	47	9.96	0.60	M2	69	11.81	0.72	64	11.41	0.63
		MANDIBLE								MANDIBLE			
I1	100	5.47	0.32	123	5.41	0.31	I1	78	6.18	0.45	91	5.99	0.42
I2	102	6.04	0.35	122	5.97	0.37	I2	78	6.44	0.42	89	6.32	0.41
C	87	6.99	0.40	87	6.66	0.33	C	73	7.92	0.53	77	7.53	0.51
P1	76	7.19	0.46	82	7.06	0.40	P1	74	8.13	0.54	84	7.81	0.54
P2	79	7.29	0.46	78	7.03	0.38	P2	78	8.64	0.53	85	8.40	0.53
M1	72	11.42	0.59	74	10.96	0.63	M1	92	10.83	0.49	116	10.50	0.47
M2	54	10.94	0.65	50	10.46	0.63	M2	67	10.72	0.60	58	10.34	0.55

Source : MNHN, Paris

Source : MNHN, Paris

Comparative Genetic Variance of Dental Size and Asymmetry in U.S. and Punjabi Twins

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ABSTRACT

Genetic variance (GV) analysis of 56 dental size and 28 bilateral asymmetry variables is based on cross cultural comparison of twin variances (U.S. Whites and Northwest Indians). Both samples exhibit substantial GV. We find monozygotes and dizygotes have unequal variances for certain traits, which invalidates conventional GV estimates. However, the pattern of environmental biases on the zygosities is very different in the two groups. Revised GV ratios that acknowledge zygosity heterogeneity, differ mainly in lessening the variability of genetic expression in the Indian twins. Bilateral asymmetry by constrast shows no GV and a high degree of environmental covariance among monozygotes.

RÉSUMÉ

La variance génétique (VG) de 56 variables de la taille des dents et de 28 variables de l'asymétrie bilatérale, est estimée à partir de la comparaison des variances intra-paire de groupes de jumeaux appartenant à deux ensembles socioculturels différents (Nord-Américains blancs et Indiens du sud de l'Inde). Les deux groupes montrent une variance génétique importante. Les écarts de variance constatés pour certains traits entre jumeaux MZ et DZ, contredisent les estimations conventionelles de la VG. Cependant, il faut remarquer que les biais environnementaux qui interviennent selon les degrés de zygosité diffèrent fortement dans les deux groupes. Les taux de VG qui rendent compte de l'hétérogénéité zygotique, diffèrent principalement par la diminution de la variabilité de l'expression génétique chez les jumeaux indiens. Par contre, on ne trouve pas de VG de l'asymétrie bilatérale, laquelle manifeste un degré élevé de covariance environnementale parmi les monozygotes.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 47-53.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

The genetic significance of odontometric traits is basic in clinical thinking and anthropology. The twin method is perhaps the best genetic analytical tool, but has rarely been applied to other than Western white populations. Comparative twin analysis in non-Western populations offers several advantages. The universality of known Western heritability patterns can be examined. Genetic interpretations of quantified populations differences can be reexamined. For example, odontometrics are frequently contrasted among human populations and differences assumed to reflect gene frequencies, yet evidence of genetic determination is largely confined to a single gene pool of Euro-American Whites. Furthermore, recent refinements in twin analysis allow detection of hidden environmental influences on the conventional genetic variance (GV) estimates.

These refined methods, applied to U.S twin data. led to fairly drastic revision of prevailing impressions (Lundstrom, 1948) of dental occlusal heritability and genetic variance (Corruccini & Potter, 1980; Potter *et al.*, 1981). Conventional GV estimates for 11 traits were high, but significant environmental biases were identified and their removal led to reduction or elimination of significant levels of GV. This approach has also been taken with U.S. twin tooth size data (Potter *et al.*, 1979), resulting in various indications of twinning stress and other biases.

The present paper considers these points, elaborating on the earlier results from U.S twins and comparing them with new data from a Northwest Indian (Punjabi) twin sample.

Material and method

Our American White twins (of middle socio-economic group) are 43 monozygotic (MZ) and 32 dizygotic (DZ) pairs from the Indiana University Twin Panel at the Medical Genetics Department. Zygosity was determined by serologic typing of ABO, Rh, MNS, Duffy, Kell, P, PGM_1, APh, Hp and HLA. These twins are predominantly in the 12-20 years age range. Their dental casts were measured using semi-automated electronic calipers with a digital system (Potter & Nance, 1976). The 150 total twin individuals consisted of 75 males and 75 females.

The twin registry of the Anthropology Department at Panjab University, Chandigarh (Sharma, 1980a *et seq.*) is being followed for study of longitudinal growth running into the tenth year (Sharma, 1978 *et seq.*). The twins are from the urban Punjabi population comprised of mostly middle to upper socio-economic levels of Indian society and enjoy good nutritional status and medical care according to Indian standards, but about 10 % of the twins are of lower socio-economic groups. It is reasonable to argue that this sample represents a broader range of environmental variation (economically, nutritionally etc.) than the U.S. twins.

Some 23 MZ and 35 DZ twin pairs were visited in their homes for dental casting (total 55 male and 61 female individuals); age ranged from 11 to 27 with a mean of 17.5. Twin zygosity was determined by A_1A_2BO, Rh, MN, Kell and Duffy serologic and PTC tasting and ABH Secretor factor markers (Sharma, 1982). Somatoscopic, anthropometric and dermatoglyphic data were also obtained but not considered in the final decision about zygosity. The dental casts were measured using sharpened digital calipers calibrated to 0.02 mm; repeat measurement error averaged just 0.1 mm or 1.4 %.

Both data sets consist of maximum mesiodistal and buccolingual (or labiolingual) dimensions of the crown of 28 secondary teeth, I1 through M2 in each quadrant. These individual lengths and breadths serve as the units of analysis; additionally, directional bilateral asymmetry (right minus left) is analyzed for each pair of antimeric measurements. We separately analyze right and left teeth of the same type here, whereas these antimeres were summed (Potter & Nance, 1976) for the U.S. twins. The very high correlation between antimeres renders this difference negligible in practice, especially when comparing ratios of variances.

Observations

Sex difference is tested in all variables by the hierarchical analysis of variance (using only the

Source : MNHN, Paris

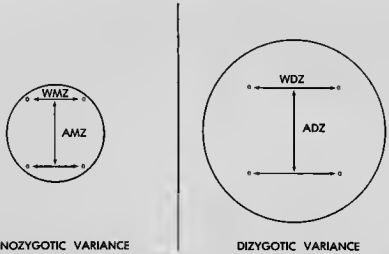

FIG. 1. — Conceptual diagram of twin variances. In this hypothetical case, within-monozygotic-pair variance is only about half that of dizygotes, suggesting significant heritability. This is an artificial result, however, because total MZ variance (TMZ = AMZ + WMZ) is also about half the TDZ. If, as represented, the among-DZ variance is not significantly more than within-DZ, there is cause to suspect relatively greater environmental covariance in MZ contrasted with DZ variances. This also would bias genetic variance estimates upward. Conversely, if TMZ were greater than TDZ then genetic variance would be underestimated.

among-pair mean squares as the error term). In all subsequent analysis males are adjusted to female by mean difference and subtracting one degree of freedom from among-pair mean squares due to significant sex difference. Tests of zygosity difference in U.S. twins were based only on the 22 like-sexed DZ pairs (Potter *et al.*, 1979); in this paper the male and female variances are computed separately and then combined.

Christian *et al.* (1974) and Kang *et al.* (1977) document some hidden assumptions, rarely acknowledged, implicit in the use of the twin model to partition variance into environmental and genetic components. First, twin zygosity must not be associated with the mean of the trait (Christian, 1979; Christian & Norton, 1977). The appropriate test (t') is based on hierarchical analysis of variance, using among-pair mean squares as the error term and the degrees of freedom are approximated. Difference between MZ and DZ means would reflect inherent biological difference associated with the type of twinning process (Christian, 1978; Christian & Norton, 1977).

Second, the standard twin model (Haseman & Elston, 1970) partitions intrapair variance into within-DZ (WDZ) and WMZ mean squares (F = WDZ/WMZ). Christian *et al.* (1974) show that the total variance within zygosities (TDZ and TMZ) must be equal for the model to hold (Fig. 1). " If the total mean squares differ more than could be expected by chance, then environmental factors were postulated as being unequal for MZ and DZ twins and the arithmetic mean (of among-twin-pair and within-twin-pair mean squares) must be used as an unbiased estimate of twin genetic variance " (Christian *et al.*, 1974). These environmental factors may possibly result from competitive or convergent influences that differ for the two twin types, both prenatally and postnatally (Kempthorne & Osborne, 1961). To test heterogeneity of total variances, one-way analysis of variance is performed, first treating twin pairs as groups of two to provide among-pair and within-pair mean squares for MZ and DZ categories, then the F' test (Christian *et al.*, 1974) compares the TMZ and TDZ. The larger is used as the numerator of a two-tailed F' test with probability level double that in usual F tables. The 0.20 probability level is used with F' to control Type II error because the test is relatively insensitive to common variance in the zygosities. Third, GV estimates will also be biased by inequality of environmental covariances of MZ and DZ twins (Christian, 1979). To test this, Christian *et al.* (1975) suggest contrasting the

Source : MNHN, Paris

mean square within and among-DZ (ADZ) pairs (F = ADZ/WDZ). If this ratio fails to appreciably exceed a value of one, " the possibility of greater environmental covariance for MZ twins should be suspected " (Christian, 1979) and " it seems unlikely that any substantial proportion of total variance is genetic " (Christian *et al.*, 1975). The test is one-tailed.

The classic GV ratio is calculated as F = WDZ/WMZ and tested for significance, provided the data pass the above three tests. If F' yields a significant result, the modified among-component ratio is used to estimate unbiased GV: F_{ac} = (WDZ + AMZ)/(WMZ + ADZ). The rationale for this test is that AMZ/ADZ is as valid and sensitive as WDZ/WMZ when total variance is heterogeneous (Christian *et al.*, 1974).

Results

None of the t' tests indicate difference in MZ and DZ mean dental dimensions in the U.S. twins. No test rejects the null hypothesis of equivalent means out of 56 trials (2 dimensions of 28 teeth) in Indian twins.

Table I gives within-pair GV ratios. U.S. twins evince fairly consistent high GV ratios which are statistically significant except for mandibular M2.

Likewise the Indian twin sample shows generally high GV ratios, but much greater fluctuation in values. Some 15 of the 56 individual values fail to reject the null hypothesis of random variation among zygosities, and these are concentrated (10 of the 15) in the lower incisor teeth and upper and lower M2. The Indian GV ratios are both higher and lower than U.S. ratios, such that no mean difference can be demonstrated; the average within-pair variance ratio is 3.76 for U.S. and 3.47 for Indian twins, not a significant difference ($p > .60$). The variability of these within-pair GV ratios, however, is significantly higher in Indians ($F = 4.8$; $p < .01$).

Many of the conventional WDZ/WMZ ratios are affected by significant total variance differences among zygosities (Table 1). Some 32 % of the F' tests reject the null hypothesis, necessitating consideration of among-component rather than within-pair variances. This occurs somewhat more frequently in Indian than American twins, more frequently in right than left teeth in Indians, and only among mandibular teeth in American twins.

Tables 1 and 2 also list instances of relatively

TABLE 1. — Within-twin-pair variance ratios for tooth diameters.

Trait		India (right)	India (left)	U.S. (right + left)	Trait		India (right)	India (left)	U.S. (right + left)
MAXILLARY					MANDIBULAR				
I1	m-d	5.09	9.07	7.98	I1	md	3.26	1.39[1]	3.42
	b-l	3.35	1.98	5.49		b-l	0.71[1, 2]	0.82[1, 2]	2.03[2]
I2	m-d	4.49	3.59	4.34	I2	m-d	3.48	4.71	2.63
	b-l	2.70[2]	1.40[1]	3.76		b-l	0.81[1, 2]	2.92	2.80[2]
C	m-d	1.37[1]	1.02[1, 2]	5.20	C	m-d	1.83[1]	3.60[2]	3.93
	b-l	4.65[1]	9.31[1]	3.13		b-l	1.54[1]	2.66[2]	3.32
P1	m-d	2.73[2]	2.14[2]	2.80	P1	m-d	1.93	2.30	4.28
	b-l	4.86	3.78	7.39		b-l	3.37[2]	5.05	3.04
P2	m-d	2.39[2]	2.63[2]	3.34	P2	m-d	2.58	1.92	3.60[2]
	b-l	4.19[2]	2.21[2]	6.91		b-l	1.21[1, 2]	4.54	5.09[2]
M1	m-d	5.49	3.43	2.26	M1	m-d	1.90	2.00	2.30
	b-l	1.17[1, 2]	3.79[2]	5.70		b-l	2.75	4.10	1.76[2]
M2	m-d	3.78[2]	1.10[1, 3]	2.59	M2	m-d	1.47[1, 2]	8.53	1.19[1]
	b-l	1.01[1]	1.35[1]	3.56		b-l	1.24[1, 2]	3.14	1.52[1]

m-d = mesio-distal diameter; b-l = bucco-lingual diameter.
1 $p > .05$ for WDZ/WMZ; null hypothesis of equal variance cannot be rejected.
2 significant total variance heterogeneity among DZ and MZ by F'; thus WDZ/WMZ is invalid.
3 $p > .10$ for ADZ/WDZ ratio. Genetic variance may be overestimated.

Source : MNHN, Paris

TABLE 2. — Among-component variance ratios for teeth with variance heterogeneity among zygosities.

Trait	India (right)	India (left)	U.S. (right + left)	Trait	India (right)	India (left)	U.S. (right + left)
MAXILLARY				MANDIBULAR			
				I1 b-l	1.36[1]	1.63[1]	2.05
I2 b-l	1.02[1]			I2 b-l	1.82		1.93
C m-d		2.13[2]		C m-d	2.31	3.15[2]	
P1 m-d	2.40	2.84		P1 b-l	2.53		
P2 b-l		2.19		P2 m-d	2.59		2.30
				b-l	2.08[2]		0.86[1]
M1 b-l	1.99	2.83[2]		M1 b-l			0.70[1]
M2 m-d	1.08[2]			M2 m-d	2.14[2]		
				b-l	2.17		

1 $p > .05$ for partition of genetic variance.
2 $p > .10$ for ADZ/WDZ ratio; genetic variance is invalidated.

TABLE 3. — Genetic variance ratios for bilateral odontometric asymmetry.

Trait	India (within-pair)	India (among-compo-nent)	U.S. (within-pair)	Trait	India (within-pair)	India (among-compo-nent)	U.S. (within-pair)
MAXILLARY				MANDIBULAR			
I1 m-d	1.51[2]	1.03[3]	0.61	I1 md	0.63[2]	0.88[3]	0.82
b-l	2.84[1, 2]	1.38[3]	0.80	b-l	0.50[2]	0.87[3]	0.40
I2 m-d	0.83		1.04	I2 m-d	1.03		1.15
b-l	1.16		1.19	b-l	1.46[3]		0.50
C m-d	1.73[3]		0.95	C m-d	2.37[1, 3]		0.94
b-l	1.27[2]	1.89[1, 3]	1.44	b-l	0.63		0.86
P1 m-d	0.78		1.79	P1 m-d	1.35		1.19
b-l	1.03		2.18[1]	b-l	1.72[2]	1.03[3]	1.10
P2 m-d	0.62[2]	1.01[3]	2.10[1]	P2 m-d	0.65		3.19[1]
b-l	0.87		1.00	b-l	0.80		1.57
M1 m-d	1.83[3]		2.70[1]	M1 m-d	2.00[3]		1.55
b-l	1.17[2]	1.71[1, 3]	1.56	b-l	0.85		1.19
M2 m-d	0.40[2]	0.69[3]	0.86	M2 m-d	0.81[2]	1.19[3]	1.34
b-l	0.79		0.64	b-l	0.42[2]	1.17	0.80

1 $p > .05$.
2 significant total variance heterogeneity among DZ and MZ by F'; within-pair estimate must be replaced by among-component.
3 $p > .10$ for ADZ/WDZ. Actual genetic variance is lower or non-existent.

greater MZ environmental covariance indicated by the ADZ/WDZ test. Indian twins fail to demonstrate significant DZ genetic partition of variance for traits, while this never occurs in U.S. twins. Table 3 shows variance ratios for bilateral dental asymmetry. As with tooth size, mean difference among zygosities is absent in every tooth. Genetic variance ratio asymmetry is very low both in Indian (average within-pair is 1.14) and U.S. twins (average 1.27). Zygosity variance heterogeneity and environmental covariance is frequently found in the Indian sample (this was never examined in the U.S. data). In all 10 traits for which Indian WDZ/WMZ ratios appreciably exceed unity, the estimate is invalidated by the F' or ADZ/WDZ test or both.

Source : MNHN, Paris

Discussion

As already well established in the literature, greater discordance in DZ than in MZ cotwins establishes significant genetic determinants for dental size by conventional (Potter & Nance, 1976). Simplistically, the within-pair variance ratios represent about 70 % heritability of tooth size traits in Indian and U.S. twins. For dental asymmetry, what little evidence there is for genetic determinance is artificially produced by a consistent tendency toward environmental convergence or competition within zygosities.

Although variance heterogeneity among zygosities is widespread in tooth size traits, the patterns of heterogeneity are unrelated in Indian and American twins: both the teeth and zygosity affected are different. Among-component estimates lead to some new nuances of interpretation, but on the average GV ratios for tooth size are robust and high. This suggests the shared intra-uterine environment generally does not appear to be a major bias in the significant GV and inferred heritability of tooth size.

The greater early prenatal stress of MZ twinning also is not a factor as judged by lack of difference in MZ and DZ means. Garn *et al.* (1979) state this MZ stress will create a wider range of AMZ variance and artificially raise heritability estimates, particularly in the presence of severe developmental anomalies caused by diabetic or hypertensive mothers. Our revised among-component estimates do not depress GV ratios by much, indicating that relatively normal prenatal environmental variations do not greatly affect tooth size. Thus the findings of Garn *et al.* (1979) may not have major implications for ordinary inter-population comparisons. Corruccini and Potter (1981) similarly demonstrate equal odontometric means among MZ and DZ twins, among normal twins and those with severe congenital abnormalities, and very low tooth size correlations with birth weight.

On the other hand, the ADZ/WDZ test raises some potential objection to straightforward interpretation of the high tooth size GV. American twins show consistently higb test ratios ($\bar{x}$ = 3.65; s.d. = 2.66) while Indian ratios are nearly balf that ($\bar{x}$ = 2.02; s.d. = 0.82); both the mean and variance are significantly different ($p > .001$). The Indian twins, arguably from a much more variable environment, indicate much more frequent MZ environmental covariance by this criterion. Clearer understanding is needed of the significance of MZ environmental covariance to all traits, as opposed to just those demonstrating MZ-DZ variance heterogeneity. The situation is also complicated by some indications of differences in zygosity influences and variances when sexes are examined separately (Potter *et al.*, 1979).

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Source : MNHN, Paris

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Source : MNHN, Paris

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3

The Pattern of Embryonic Tooth Initiation in Reptiles

B. WESTERGAARD

ABSTRACT

Histological development of the dentition (lower jaw) was studied in several reptilian species: the tuatara *Sphenodon punctatus*, the alligator *Alligator mississippiensis*, the gecko *Cnemaspis kandiana*, the sand lizard *Lacerta agilis*, and the slow worm *Anguis fragilis*. The first light microscopical trace of tooth formation was a localized thickening of the oral epithelium (" placode stage "). Tooth initiation seems to originate and spread in the epithelium. First, one tooth appears at the front of the jaw anlage, and further teeth develop anteriorly, posteriorly and interstitially: the number and sites of future functional tooth positions correlating with and possibly being controlled by differential jaw growth (the **Tooth Position Theory**; Westergaard, 1983). In this way interspecific differences in dentitional patterning may be produced, sbowing that tbe embryonic dental system is characterized by great evolutionary plasticity. No regular alternation is found in the embryonic initiation pattern, with the possible exception of the tuatara. Computer maps were generated from measurements of tooth outlines in the histological sections, and tooth sizes and distances were calculated. The figures are compatible with the idea of a size and/or stage dependent inhibition zone around each forming tooth. Interspecific comparisons show that several early teeth may be bomologized on tbe basis of their relative positions and initiation times.

RÉSUMÉ

Le développement histologique de la dentition (mâchoire inférieure) est étudié chez différentes espèces de reptiles : le tuatara *Sphenodon punctatus*, l'alligator *Alligator mississippiensis*, le gecko *Cnemaspis kandiana*, le lézard des sables *Lacerta agilis* et l'orvet *Anguis fragilis*. La première trace, au microscope, de la formation d'une dent consiste en un épaississement localisé de l'épithélium oral (« stade placode »). La formation de la dent semble débuter dans l'épithélium puis s'y répandre. D'abord une dent apparaît á l'avant de l'embryon de mâchoire, et les dents suivantes se développent á l'avant, á l'arriére et en position intermédiaire, le nombre et l'emplacement des futures positions fonctionnelles des dents étant liés á la croissance différentielle de la mâchoire, et peut-être controlés par elle (« the **Tooth Position Theory** »; Westergaard, 1983). Il peut en résulter des différences interspécifiques dans le scbéma de la série dentaire, ce qui montre que le système dentaire embryonnaire est doué d'une grande plasticité évolutive. Il n'a pas été observé d'alternance réguliére dans le sehéma d'apparition des premiers bourgeons dentaires, sauf peut-être pour le tuatara. Les contours dentaires mesurés sur des coupes histologiques ont été introduits dans l'ordinateur, pour obtenir des sehémas á partir desquels la taille des dents et les distances interdentaires ont été calculées. Les chiffres sont compatibles avec le concept d'une zone d'inhibition autour de chaque dent en formation, dépendant de la taille et/ou du stade d'évolution. Des comparaisons interspécifiques montrent que plusieurs dents précoces peuvent être considérées comme homologues d'aprés leurs positions relatives et l'époque du début de leur formation.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris*, (série C) **53** : 55-63.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

Most recent investigations on early dental development have concentrated on the formation of individual teeth, and then only in a very few species, notably laboratory mammals (see reviews by Hurmerinta, 1982; Ruch *et al.*, 1983; Slavkin & Zeichner-David, 1981). The process of dentitional pattern formation has evoked only limited interest (Berkovitz, 1977, 1978; Edmund, 1960; Lumsden, 1979; Osborn, 1971, 1973, 1974, 1977, 1978, 1984; Reif, 1984; Westergaard, 1980, 1983; Westergaard & Ferguson, 1986, 1987). The dental specializations of most mammals (few teeth, with only one set of replacement teeth, marked heterodonty, etc...) suggest, however, that mammals are not ideal for studying the basic principles of dentition patterning. In particular, the dentitions of rodents and rabbits (although the objects of most dental studies) are probably too specialized.

Unfortunately, detailed information about the early initiation pattern of non-mammalian dentitions is available only for the rainbow trout *Salmo gairdneri* (Berkovitz, 1977, 1978), and the reptiles *Crocodylus porosus* (Rôse, 1894; Woerdeman, 1919), *Chalcides ocellatus* (Woerdeman, 1919) and *Lacerta vivipara* (Osborn, 1971). As no generalized pattern emerges from these studies, it was decided to investigate the embryonic dentition development in several reptilian species. The present paper summarizes the results of early dentition formation in the lower jaw. More complete descriptions of both lower and upper jaws are published elsewhere (Westergaard & Ferguson, 1986, 1987, in preparation; Westergaard, in preparation).

Material and method

Histologically sectioned and stained specimens of close series of reptilian embryos were obtained for: the tuatara *Sphenodon punctatus* (Department of Biology, King's College, London; now transferred to Department of Zoology, University of Cambridge), the alligator *Alligator mississippiensis* (Department of Basic Dental Sciences, University of Manchester), the gecko *Cnemaspis kandiana*, the sand lizard *Lacerta agilis*, and the slow worm *Anguis fragilis* (Institute of Cell Biology and Anatomy, University of Copenhagen). For each species hand maps of developing dentitions were drawn directly from the slides through a light microscope. Comparison of the relative developmental stages and positions of teeth in close series of embryonic stages enabled the establishment of tooth identities within and between species, as well as tooth initiation sequences. A special computer program was developed, using measurements from the midline of transverse sections to the outer surfaces of teeth to plot precisely scaled two-dimensional dentition maps of selected embryos. In this way the sizes and distances between teeth could be observed and calculated.

Results

The first indication of tooth development was a localized thickening of the epithelium (placode stage, see Westergaard & Ferguson, 1986). At this stage, the mesenchyme is uniformly dense beneath the oral epithelium. A localized condensation of mesenchymal cells rapidly appears beneath the epithelial thickening, but placodes of the first two teeth may form before any traces of mesenchymal condensations are visible (slow worm, Plate Ie). The earliest teeth are initiated from oral surface epithelium, before the dental lamina is formed (Plate Ia & c). In some species (tuatara, alligator, gecko), several early teeth project markedly from the jaw surface (Plate Ib & c), before being resorbed (Plate Id & h) or shed. In other species, a few early teeth project, but only slightly (Plate If), and only for a short period (sand lizard, slow worm). In some species all teeth are at some stage connected to the ingrowing dental lamina (gecko, sand lizard, slow worm; Plate Ig & h), whereas in others the earliest teeth develop independent of the lamina (tuatara, alligator; Plate Ib & c): illustrating that teeth are not necessarily formed from a dental lamina. All functional teeth develop, however, from the lamina.

In all lower jaw halves only one tooth (the dental determinant *sensu* Osborn, 1973) is present at the beginning of dental development, and

Source : MNHN, Paris

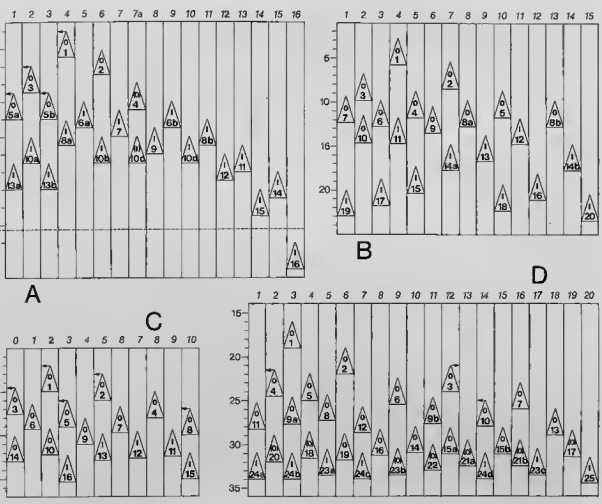


FIG. 1. — Diagrams of embryonic tooth initiations (tips of triangles) establishing the lower jaw tooth positions present at hatching, indicated by italic numbers (abcissa). Arrows signify that teeth are placed in the direction of the arrow compared to the next tooth generation, making the tooth family rather arbitrary (compare Fig. 1A with Fig. 2B). Small numbers in triangles represent tooth initiation sequence. Capital numbers: 0 = resorptive teeth, 1 = first set of functional teeth. Brackets indicate variability, as some teeth are either resorptive, transitory/normally functioning, or not formed.

A, Tuatara. Ordinate = rough estimate of weeks after egg laying. Position *7a* is not present at hatching, if tooth 4 is resorptive and tooth 10c is not formed.

B, Sand lizard. Ordinate = days after egg laying.

C, Slow worm. Ordinate = days after the latest stage without visual odontogenic tissue mobilization. Position 0 is not present at hatching.

D, Alligator. Ordinate = days after egg laying. Total tooth initiation pattern up to hatching in Westergaard & Ferguson (1987, fig. 4).

always at the front of the jaw anlage. The next tooth is initiated posterior to the first one. Additional teeth develop both anterior to, between, and posterior to, the first two: the numbers, positions, times and sequences varying between species, thus resulting in the different numbers of tooth positions observed at hatching (Fig. 1). Generally, later initiated teeth are bigger than earlier ones and develop closer to their smallest, most mature neighbours: showing that the placing of tooth initiation is correlated with the sizes and/or developmental stages of earlier teeth (Fig. 2A). Some of the first teeth, different numbers in different species (Fig. 1), are resorbed or shed without becoming functional. Replacement teeth are formed from the inner end of the

Source : MNHN, Paris

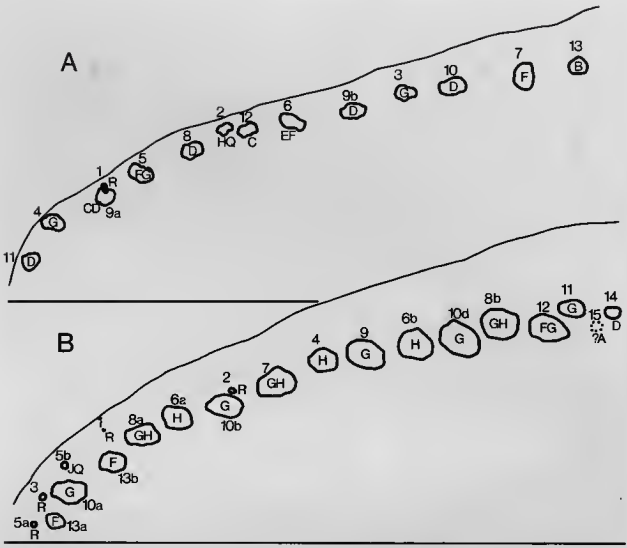


FIG. 2. — Computer-generated maps showing horizontal projections of embryonic dentitions in lower jaw halves. Numbers represent tooth initiation sequences, with small letters added alphabetically from the jaw tip if more teeth initiate simultaneously (see Fig. 1). Capital letters indicate progressive tooth developmental stages (further details in Westergaard & Ferguson, 1986): ?A = (inconspicuous) localized thickening of odontogenic epithelium, without mesenchymal condensation (placode stage). A = localized thickenings of odontogenic epithelium and mesenchyme, tooth papilla concave or straight (bud stage). B-E = subsequent stages of relative tooth germ heights before dentine formation. F = first indication of dentine matrix. G-J = subsequent stages of dentine formation. Q = inner enamel epithelium degenerated, little or no resorption of tooth matrix, numerous large cells in pulp. R = resorption of tooth matrix advanced, few or no large cells in pulp.

When the determination of tooth stage is difficult, two stages are included in the presentation.

A, Alligator. Ferguson (1985) stage 19 day 27 (compare with Fig. 1D). Two tooth positions have formed between teeth 1 and 2, and three positions between teeth 2 and 3. Tooth 1 is the only one with a successor tooth (9a). Mapped jaw length: 2.4 mm.

B, Tuatara. Dendy (1899) stage R (compare with Fig. 1A). In this jaw half tooth 10c is not formed and 4 becomes functional. Tooth families *1* to *4* are somewhat arbitrarily defined, but a nearly regular alternation is found between the first series of older (teeth 3, 1, 2, 4, 6b, 8b, 11 & 14) and younger teeth (5a, 5b, 6a, 7, 9, 10d, 12 & 15). Mapped jaw length: 4.7 mm.

Source : MNHN, Paris

TABLE 1. Homologization of embryonic teeth in the different species on the basis of relative tooth positions and initiation times. Numbers identify teeth of each species by their initiation sequence (compare with Fig. 1).

Tooth name	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*	*o*	*p*	*q*	*r*	*s*
sand lizard	1	2	3	4	5	6	7	8a	8b	9	10	11	12	13	14a	14b	15	16	20
slow worm	1	2	3	5	4	6	—?	7	8	9	14	10	11	12	13	15	16	?	—?
gecko	1	2	3	5	4	7a	8	7b	6	10	13a	12	11	13b	15	9	17	16a	16b
tuatara	1	2	3	6a	4	5b	5a	7	6b	10b?	10a	8a	9	10c?	?	8b	—	?	11
alligator	1	2	4	5	3	9a?	11	6	7	8	20	?	10	9b	12?	13	18?	15b	17

dental lamina, when this has reached a certain distance from the earlier tooth generation. This distance is small if the earlier tooth has started degeneration. It is sometimes difficult to delimit obvious tooth families (: different tooth generations at the same tooth position), which seem to be rather arbitrarily defined in early development (Figs. 1 and 2B).

Although variation between species is pronounced, a generalized pattern of tooth initiation can be recognized, allowing interspecific comparisons/identifications of many early teeth on the basis of relative initiation times and positions (Table 1).

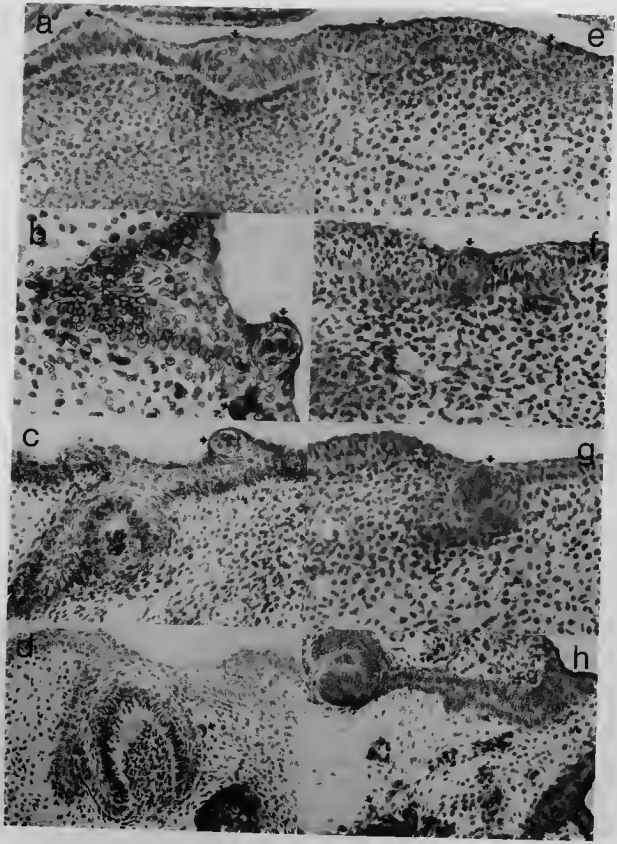
DISCUSSION

While a few reports indicated that the first epithelio-mesenchymal tooth interactions commence in the oral epithelium (Dryburg, 1967; Lumsden, 1984; Miller, 1969, 1971), the current consensus has favoured the mesenchyme as the directing force in early tooth development (Kollar & Baird, 1969, 1971). Also, formation of a dental lamina is often assumed to be a prerequisite for tooth initiation (Ruch *et al.*, 1983). Recently, however, Mina & Kollar (1987) demonstrated experimentally that the early mandibular epithelium controls tooth initiation in mice, thus determining the fate of the associated mesenchyme. The results reported here show that at least two epithelial thickenings may be present before there are any visible mesenchymal condensations, suggesting that the tooth initiation process originates and spreads in the epithelium. Furthermore, a few early teeth develop independent of the dental lamina in some species, but only in connection with a dental lamina in other species, demonstrating that a certain area of oral epithelium is capable of making teeth (nonlamina teeth being nonfunctionnal), regardless of whether it is on the surface or submerged as a dental lamina.

Except for Röse's (1894) results, previous studies on non-mammalian vertebrates showed that the dentition pattern was established on the basis of regularly alternating tooth initiations in early development, starting either at the front (Berkovitz, 1977, 1978; Woerdeman, 1919) or in the middle of the jaw anlage (Osborn, 1971). In the present investigation only the data from the tuatara come close to the conception of a regularly alternating embryonic dentition (Fig. 1). Very likely, the developmental schemes of Woerdeman (the **Odontostichos Theory**, 1919), Edmund (the **Zahnreihe Theory**, 1960), and Osborn (the **Tooth Family Theory**, 1971) were based on misinterpretations of data (Westergaard & Ferguson, 1986). Also, the generally accepted idea of naturally demarcated families of tooth generations formed at each tooth position in the jaw seems to be an illusion in early development. Thus, the value of Osborn's (1971, 1973) **Tooth Family Theory**, which makes tooth families the important units of dentitions, is questionable when it comes to explaining early dentition development.

The number and places of tooth positions seem to be dependent on the genetically controlled differential growth of the embryonic jaw anlage and the dental lamina, creating more or less space around already existing teeth for new teeth to form. In some cases a tooth which is initiated from the dental lamina at or close to the

Source : MNHN, Paris



Source : MNHN, Paris

same jaw position as an earlier tooth, and so at this stage would be judged as the replacement tooth, may later move to a neighbouring position and establish its own tooth family. The developmental scenario just outlined, linking the formation of tooth positions with jaw growth, was named the **Tooth Position Theory** (Westergaard, 1983).

The fact that new teeth are initiated closer to their smallest and most mature neighbours is compatible with the existence of some kind of inhibition zone around each developing tooth, as proposed by Osborn (1971). Westergaard & Ferguson (1987) put forward a progress zone model to explain the pattern of tooth initiation, inhibition zones being caused by changing positional values following the recruitment of cells into the epithelial placodes. In accordance with the Tooth Position Theory, while early dentition ontogeny within each species investigated was precisely controlled with little variation, the differences between species (Fig. 1) illustrate tbat the embryonic dental system is characterized by great evolutionary plasticity.

Evidence from mammals suggests that the mechanism controlling the number and positions of teeth is different from the one specifying tooth morphology (Butler, 1979, 1982; Westergaard, 1980; see also Westergaard & Ferguson, 1987). Traditionally, a mixture of number, position and morphology has been used as a basis for establishing tooth homology (: teeth derived from the same tooth in the common ancestor). In recent years many suggestions have been made for using morphology alone (Osborn, 1978; Schwartz, 1982). However, morphology may change gradually along the tooth row; several teeth may share the same morphology, belonging to one so-called tooth class (*sensu* Osborn, 1978); some teeth show characteristics of different classes (" mixed morphology ") and are therefore not easily placed into either; and simple genetic or hormonal changes may cause identical morphological changes at several tooth positions (Grüneberg, 1965; Gabrion & Chibon, 1973). Thus, even for heterodont dentitions, morphology is not a good discriminator of individual tooth elements. Furthermore, the limits of tooth classes are often arbitrary and extremely variable between species, sometimes even between closely related ones, with identical numbers of teeth (Butler, 1979; Westergaard, 1980). In conclusion, relative initiation position (and number) is generally a more reliable criterion for tooth homology. Obviously, morphology is of no use in homologizing the teeth of more or less homodont dentitions. In the case of reptiles, it seems that the patterns of tooth initiation show some basic similarities between species, thus allowing relative tooth positions and initiation times to be used for the homologization of several early teeth (Table 1).

PLATE 1. — Histological sections showing development of lower teeth 1 and 2 in the tuatara (a-d) and the slow worm (e-h). Figures at the end of the legends below indicate the vertical heights of micrographs.

a, Bud stages of teeth 1 (left arrow) and 2 (right arrow). The papilla of tooth 1 is not visible on this section. Note that both teeth project beyond the jaw surface. No dental lamina has formed yet. Dendy (1899) stage P. 280 μm.

b, Tooth 1 at a later stage, with dental epithelium (upper arrow) projecting approximately 35 μm beyond the jaw surface, close to the dental lamina. Dentine tooth rudiment is seen as a dark shadow below the jaw surface (lower arrow). Dendy stage Q. 170 μm.

c, Tooth 2 at a later stage, with dental epithelium (arrow) projecting a little distance from the dental lamina and the developing replacement tooth (10b). Dendy stage Q. 360 μm.

d, Tooth 2 lying as a resorbing dentine rudiment in the mesenchyme (arrow) close to replacement tooth 10b. Dendy stage R. 400 μm.

e, Placode stages of teeth 1 (left arrow) and 2 (right arrow). The thickened epithelial placodes are not yet associated with condensed mesenchymal papillae. Note that none of the teeth project from the jaw surface. The dental lamina has not formed yet. Keibel (1906) stage fig. 32f. 3 days PNO (post the latest stage with no visual mobilization of odontogenic tissues). 200 μm.

f, For a few days tooth 1 projects slightly from the jaw surface (arrow), before sinking into the mesenchyme. Keibel stage fig. 32g. 6 days PNO. 180 μm.

g, Tooth 2 (arrow) never projects from the jaw surface. The tooth germ is situated on the lateral part of the early ingrowing dental lamina. Keibel stage fig. 32 g. 6 days PNO. 185 μm.

h, Resorbing dentine rudiment of tooth 2 (arrow) lying deep in the mesenchyme at some distance from its replacement tooth (13) and the dental lamina. The former connection between tooth and lamina is indicated by a bulge on the lateral lamina epithelium midway between tooth 13 and the jaw surface. Embryo slightly advanced compared to Keibel stage fig. 32h. 16 days PNO. 230 μm.

Source : MNHN, Paris

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Source : MNHN, Paris

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Comparison of Growth and Cell Proliferation Kinetics during Mouse Molar Odontogenesis *in vivo* and *in vitro*

N. AHMAD & J. V. RUCH

ABSTRACT

The growth of embryonic first lower mouse molars grown *in vitro* is slow and reduced in comparison with the *in vivo* evolution: the volume of teeth removed on day 15 and 16 of gestation and cultured for 6 days never exceeded the volume reached at day 18 *in vivo*. The volume of teeth removed on day 17 and 18 and cultured for 6 days either remained constant or decreased. The appearance of post-mitotic odontoblasts and ameloblasts was delayed *in vitro*. This behaviour might be correlated with a lengthening of the cell cycle (TC). *In vitro* the average durations of TC (established by the percent labelled mitosis technique) were respectively 17.4-20.2 hr and 19.1-19.4 hr for preodontoblasts and preameloblasts. *In vivo* the corresponding TC were 13.9 hr and 13.5 hr. The coordination of mitotic activities of preodontoblats and preameloblasts existing *in vivo* was maintained *in vitro* and therefore seemed to require intradental control mechanisms. Non specific extradental serum factors may affect the duration of TC.

RÉSUMÉ

La croissance des premières molaires inférieures d'embryons de souris cultivées *in vitro* est ralentie par rapport à la croissance *in vivo*. Le volume des dents prélevées aux jours 15 et 16 de la gestation et cultivées pendant 6 jours ne dépasse jamais le volume atteint *in vivo* au jour 18. Le volume des dents prélevées les jours 17 et 18 et cultivées pendant 6 jours reste constant ou diminue. L'apparition d'odontoblastes et d'adamantoblastes postmitotiques est retardée *in vitro*. Ce comportement est corrélé avec l'allongement de la durée du cycle cellulaire, TC (déterminée à l'aide de la méthode des mitoses marquées) : TC est de l'ordre de 19 heures *in vitro* et de 13.5 heures *in vivo*. La coordination des activités mitotiques des préodontoblastes et préadamantoblastes existant *in vivo* est préservée *in vitro* et procède de l'existence de mécanismes de contrôle intradentaires. Des facteurs extracellulaires peuvent agir sur la durée du cycle.

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Introduction

The respective role of genetic and environmental factors in tooth development is still controversial. The crown size and morphology of a specific tooth is a function mainly of the number of post-mitotic odontoblasts and ameloblasts and of their spatial distribution. The metabolic activities of these cells, which control the amount of dentine and enamel, also play important roles. It seems likely that genetic factors determine the number of functional cells as well as their specific metabolic activities. The involved epigenetic effectors are not identified. However, we know environmental factors which may affect both the number of functional odontoblasts and ameloblasts and their activities: mitostatic drugs disturb tooth morphogenesis and cytodifferentiations (Ruch & Karcher-Djuricic, 1971; Nogueira, Stene & Koppang, 1981). Hypervitaminose A as well as hypovitaminose (Hurmerinta, Thesleff & Saxen, 1980) and ascorbic acid deficiency (Schiltz, Rosenbloom & Levenson, 1977) were shown to impair odontogenesis. Transferrin appeared to be a necessary serum protein for the morphogenesis of bud and early cap staged teeth (Thesleff & Partanen, 1984).

At a morphological level, odontogenesis is initiated during the early stages of cranio-facial development. The mitotic indices and their temporo-spatial evolution as well as the cell cycle parameters (using the percent labelled mitosis technique) have been established during dental lamina formation, bud and bell stages of first lower mouse molars (Osman & Ruch, 1975, 1976, 1978): the mitotic activity of the oral epithelial cells involved in dental lamina formation was not increased in comparison with the activity of adjacent oral epithelial cells. The dental lamina formation resulted from modifications in orientation of the mitotic spindle: before dental lamina formation, the preferential orientation was parallel to the surface of the oral epithelium. During dental lamina formation, the spindles became perpendicular and the daughter cells were superposed. At day 11 (initiation of dental lamina formation) the mean duration of the cell cycle (TC) was respectively 10 and 9 hr for epithelial and mesenchymal cells. The mean durations of G_1 (TG_1) were respectively 1.2 and 2.1 hr.

The analysis of serial frontal sections of mandibular arches of 14 to 18-day old mouse embryos demonstrated: 1) a significant dissociation between the values of mitotic indices of inner and outer dental epithelium; the indices of the outer epithelium decreased rapidly while the indices of the inner epithelium (potential ameloblasts) remained high; 2) regional variations of mitotic activity of inner dental epithelium which seemed to be correlated with the cusp formation. During odontogenesis TC increased mainly by the lengthening of TG_1: on day 16, TC of molar epithelium and mesenchyme were 13.5 and 13.9 hr respectively and the duration of TG_1 were 4 and 4 4 hr respectively.

The terminal differentiation of odontoblasts occurred according to a specific temporo-spatial pattern. In the first lower molar of Swiss mice, the first overtly differentiated odontoblasts were found at day 18 at the tip of the principal cusps, and progressively new functional odontoblasts emerged toward the basal parts of the cusps (Ruch, Karcher-Djuricic & Thiebold, 1976). It seemed that, after the last physiological division, the daughter cells were superposed and only the cell in relation with the inner dental epithelium overtly differentiated. The terminal differentiation of ameloblasts occurred according to the same spatial pattern as for odontoblasts, but was delayed for 24-36 hr (Ruch, 1984).

It is well known that both tooth morphogenesis and dental cytodifferentiation may occur *in vitro*. However mini-teeth will differentiate and the crown morphogenesis may be disturbed. The comparison of cell proliferation kinetics *in vitro* and *in vivo* may improve our understanding of the role of cell kinetics during tooth morphogenesis and cytodifferentiation.

Material and method

First lower molars of laboratory raised Swiss mice were removed on days 15, 16, 17, 18, 19, 20 and 21 (vaginal plug = day 0). Teeth removed on days 15, 16, 17 and 18 were cultured respectively during 1 to 6 days. The teeth were cultured either on a semi-solid coagulum formed of 2 parts of Hanks' solution, 1 part fetal calf serum, 1 part embryonic chick extract and

Source : MNHN, Paris

6 parts cock plasma (Ruch, Karcher-Djuricic and Thiebold, 1976) or on Millipore filters in presence of DMEM supplemented with 292 μg of glutamine and 10 % fetal calf serum. All the teeth were fixed in Bouin's, paraffin embedded, cut in 5 μm serial sections and stained with Mallory's. The volume of the teeth growing *in vivo* and *in vitro* was established by measuring the surfaces of the serial sections using a modular image analysing system (MPO/AM 02 Kontron).

The chronology of the appearance of polarizing post-mitotic odontoblasts and ameloblasts was determined during *in vivo* and *in vitro* evolution by careful analysis of the serial sections. The mitotic indices of preodontoblasts, preodontoblasts plus odontoblasts, preameloblasts, preameloblasts plus ameloblasts were established: alternate sections were analyzed completely using a Leitz oil immersion planapo × 100 objective. The percent of labelled mitosis (PLM) for preodontoblasts and preameloblasts were established for 16-day molars: After 2 and 6 days *in vitro* 1μCi ^{3}H TdR (25Ci/mM CEA, France) was added for 15 min. to the culture media. After labelling, the teeth were washed 3 times in DMEM and then post-cultured up to 24 hr. Sequential fixations were performed 1 to 24 hr post-labelling and the slides were processed for radioautography using Kodak AR10 stripping film. The exposure was 14 days. The slides were developed in D19 at 20°C for 4-5 min. and post-stained with Mayers Hämalun. Alternate sections were analyzed completely and each mitosis viewed carefully using a Leitz oil immersion × 100 objective. At least 100 mitosis were recorded for each time point.

All data-mitotic indices, determination of the volume, chronology of the appearing of post-mitotic cells and the PLM, result from the analysis of 3 different teeth for each stage and culture duration.

After the angular transformation of mitotic indices, means and standard deviations have been established and one way analysis of variance was performed.

Results

In vivo the realization of the specific cusp pattern progressed between days 15 and 21. Teeth grown on semi-solid coagulum demonstrated normal, but delayed constitution of the cusps. Teeth grown on Millipore filters demonstrated abnormal crown morphology (Fig. 1).

As far as the evolution of the volume and of the mitotic indices are concerned, no statistical differences existed between both culture techniques. The chronology of appearance of post-mitotic odontoblasts and ameloblasts as well as the PLM data were also the same. For these

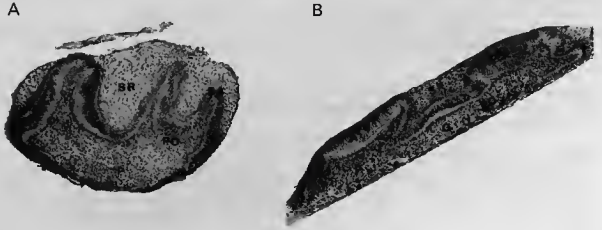

FIG. 1. — Histological sections of mouse first lower molars removed on day 17 and cultured for 4 days .
A, on semi-solid medium the cusp pattern is well preserved; B, on Millipore filters the crown morphogenesis is disturbed.
A = ameloblasts; O = odontoblasts; P = dental papilla; PA = preameloblasts; PO = preodontoblasts; SI = stellate reticulum.

Source : MNHN, Paris

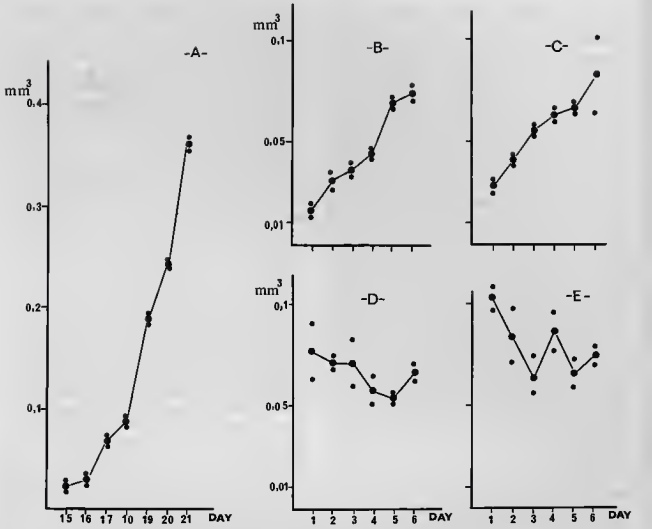

FIG. 2. — Evolution of the volume of mouse first lower molars.
A, Teeth growing *in vivo* from day 15 to day 21; B, C, D, E, Teeth growing *in vitro* during 1 to 6 days. The teeth were respectively removed on day 15 (B), 16 (C), 17 (D) and 18 (E). In each case 3 different teeth were measured.

reasons we compared, in this paper, the data of teeth grown on semi-solid medium with the data of molars grown *in vivo*.

Evolution of the volume

In vivo the volume increased rapidly from day 15 to day 21 (Fig. 2). *In vitro* the volume of day 15 and 16 molars increased slowly, and after 6 days the volume was not significantly different from the volume reached at day 18 *in vivo* (Fig. 2). The volume of molars removed on days 17 and 18 and cultured up to 6 days either remained more or less constant or decreased. Again the maximum volume was not different from the volume reached on day 18 *in vivo* (Fig. 2).

Chronology of dental cytodifferentiations

Table 1 summarizes our observations. *In vitro* the appearance of post-mitotic odontoblasts and ameloblasts was delayed for 1-2 days in comparison with the chronology existing *in vivo*.

Evolution of the mitotic indices

Table 2 and 3 summarizes the angular transformations of the mean mitotic indices and the

Source : MNHN, Paris

TABLE 1. Chronology of dental cytodifferentiations of mouse first lower molars removed on day 15, 16, 17 or 18 and grown on semi-solid medium during 1 to 6 days.
AF = functional ameloblasts; AP = polarized ameloblasts; OF = functional odontoblasts; OP = polarized odontoblasts;

Stage	Days in culture 1	2	3	4	5	6
15					OP	OF + AP
16				OP		OF + AP
17		OP		OF + AP		OF + AF
18	OF + AP			OF + AF		

TABLE 2. Angular transformations of mean mitotic indices and standard deviations X 1000 of dental cells during *in vivo* evolution of first lower molars from day 15 to day 21. The differences between the mitotic indices of PO and PO + O; PA and PA + A resulted from the appearance of post-mitotic cells.

DAY	PO	PO + O	PA	PA + A
15	239,6 ± 1,88	239,6 ± 1,88	178,9 ± 5,85	178,9 ± 5,85
16	207,1 ± 4,54	207,1 ± 4,54	190,2 ± 4,05	190,2 ± 4,05
17	180,5 ± 3,31	180,5 ± 3,31	201,7 ± 3,77	201,7 ± 3,77
18	161,9 ± 4,61	155,8 ± 1,42	155,5 ± 2,55	155,5 ± 2,55
19	135,1 ± 2,94	120,7 ± 3,48	141,1 ± 4,25	136,1 ± 2,57
20	84,4 ± 5,19	64,9 —	137,3 ± 2,74	78,3 ± 1,51
21	74,5 ± 3,06	33,2 ± 3,45	122,5 ± 9,1	50,1 ± 3,17

standard deviations during *in vivo* and *in vitro* evolution. Fig. 3 illustrates the evolution (*in vivo* and *in vitro*) of the mitotic indices of preodontoblasts plus odontoblasts and preameloblasts plus ameloblasts. Table 4 summarizes the results of the statistical comparisons. We compared the results of molars removed on day 15 and cultured for 1 day with the data of day 16 molars and so on. The main results are the following: during the first days in culture the mitotic indices were either lower or not significantly different from the indices existing *in vivo* at comparable stages. During the 2 or 3 last days in culture the mitotic indices were always significantly higher than those existing *in vivo*. These results corroborate the delayed appearance of post-mitotic odontoblasts and ameloblasts.

Source : MNHN, Paris

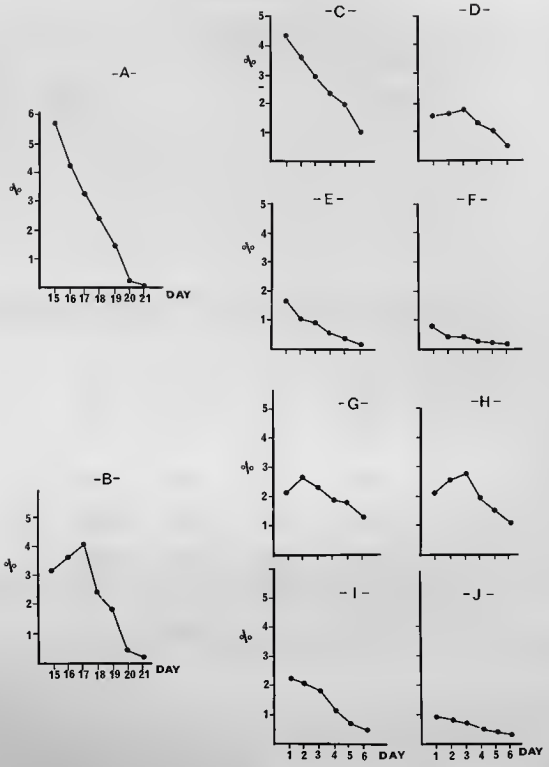

FIG. 3. — Evolution of the mitotic indices of preodontoblasts plus odontoblasts and preameloblasts plus ameloblasts of teeth growing *in vivo* from day 15 to day 21 (A, B) and *in vitro* during 1 to 6 days (C-J).
A, preodontoblasts plus odontoblasts; B, preameloblasts plus ameloblasts; C-F, preodontoblasts plus odontoblasts of teeth removed respectively on day 15 (C), 16 (D), 17 (E) and 18 (F); G-J, preameloblasts plus ameloblasts of teeth removed respectively on day 15 (G), 16 (H), 17 (I) and 18 (J).

Source : MNHN, Paris

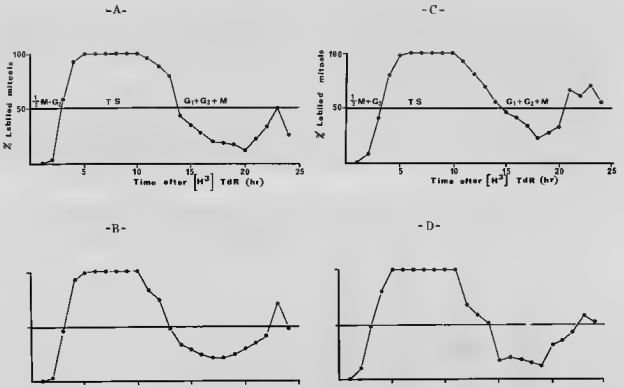

FIG. 4. — PLM for preodontoblasts and preameloblasts of first lower molars removed on day 16 and cultured either for 2 (A, B) or 6 days (C, D) before ^{3}H TdR labelling. A, C, preodontoblasts; B, D, preameloblasts.

CELL CYCLE PARAMETERS

The PLM technique (Fig. 4) allows the estimation of TC for the preodontoblasts and preameloblasts of molars removed on day 16 and cultured for 2 and 6 days. The respective durations were 20.2 and 19.4 hr after 2 days in culture and 17.4 and 19.1 hr after 6 days. The TC of *in vivo* growing teeth were 13.9 and 13.5 hr respectively at day 16 (Osman & Ruch, 1978).

DISCUSSION

Several experimental results (Ruch, Karcher-Djuricic & Gerber, 1972; Ruch, Karcher-Djuricic & Thiebold, 1976) led to the hypothesis that odontoblast's and ameloblast's genetic programs may determine a minimal number of cell cycles before overt differentiation can be triggered by specific epigenetic matrix mediated interactions (Ruch, 1985; Karcher-Djuricic, Staubli, Meyer & Ruch, 1985). The present data seem to agree with this hypothesis. The delayed appearance of post-mitotic odontoblasts and ameloblasts *in vitro* is explained by the lengthening of TC:

During *in vivo* evolution (day 16) the average TC is 14 hr. Respectively 5-6 and 6-7 cell cycles may exist between day 15 and the appearance of the first post-mitotic odontoblasts on day 18 and the first post-mitotic ameloblasts on day 19. *In vitro* TC lasts about 20 hr and to realize 5-6 or 6-7 cell cycles respectively (for day-15 molars), 5 or 6 days are required. The genetic program controlling the number of cell cycles and the coordination of mitotic activities of preodontoblasts and preameloblasts are maintained *in vitro*. Intradental autonomous control mechanisms exist. Previous data (Olive & Ruch, 1982) stressed the importance of cell-matrix interactions. Non specific serum factors may however affect the duration of the cell cycle. Quantitative and/or qualitative physiological modifications of

Source : MNHN, Paris

such factors may explain the progressive lengthening of the cell cycle *in vivo*. The absence of a similar evolution *in vitro* might be explained by the relative stability of the culture media.

Dissection of the molars and the onset of the culture disturb the initial kinetic behaviour. Complementary investigations are required to determine the labelling index during this period.

The *in vitro* conditions do not allow a normal increase of the dental volume, and the volume corresponding to day 18 molars is not exceeded. The lengthening of TC contributes to the reduction of growth. However, it will be necessary to compare the evolution of the growth fraction *in vivo* and *in vitro* and to determine the importance of cellular death.

Finally, the cell proliferation kinetics *in vitro* are the same in the case of normal or abnormal crown morphogenesis. Differential mitotic activities controlled by cell matrix interactions seem to be involved in crown morphogenesis (Osman & Ruch, 1976). However, this necessary factor is

TABLE 3. Angular transformations of mean mitotic indices and standard deviations X 1000 of dental cells of day 15, 16, 17 and 18 mouse first lower molars grown on semi-solid medium during 1 to 6 days. A = ameloblasts; O = odontoblasts; PA = preameloblasts; PO = preodontoblasts.

		PO	PO + O	PA	PA + A
15	+ 1	209,6 ± 3,96	209,6 ± 3,96	146,1 ± 3,18	146,1 ± 3,18
	+ 2	190,7 ± 2,56	190,7 ± 2,56	162,3 ± 3	162,3 ± 3
	+ 3	173,3 ± 5,99	173,3 ± 5,99	153 ± 2,39	153 ± 2,39
	+ 4	154,4 ± 5,03	154,4 ± 5,03	137,7 ± 1,96	137,7 ± 1,96
	+ 5	142,6 ± 2,79	141,1 ± 4,05	135,4 ± 3,03	135,4 ± 3,03
	+ 6	113,9 ± 4,13	102,1 ± 4,3	130,1 ± 5,27	115,3 ± 5,55
16	+ 1	123,9 ± 2,04	123,9 ± 2,04	147,5 ± 3,62	147,5 ± 3,62
	+ 2	126,8 ± 4,79	126,8 ± 4,79	160,6 ± 2,69	160,6 ± 2,69
	+ 3	130,6 ± 3,46	130,6 ± 3,46	164,5 ± 1,81	164,5 ± 1,81
	+ 4	116,3 ± 2,86	113,4 ± 2,12	139,1 ± 4,73	139,1 ± 4,73
	+ 5	107,6 ± 5,07	102,4 ± 6,09	131,2 ± 5,62	122,7 ± 0,63
	+ 6	79,5 ± 5,52	72,1 ± 6,12	122,7 ± 6	105,1 ± 6,2

		PO	PO + O	PA	PA + A
17	+ 1	128,6 ± 2,91	128,6 ± 2,91	147,9 ± 6,64	147,9 ± 6,64
	+ 2	109,3 ± 3,09	103,9 ± 1,13	143,1 ± 7,66	143,1 ± 7,66
	+ 3	105 ± 6,14	96 ± 8,26	153,8 ± 5,26	134,2 ± 9,12
	+ 4	101,4 ± 2,33	77 ± 2,8	146,1 ± 3,1	103,5 ± 7,49
	+ 5	87 ± 8,22	62,6 ± 2,44	126,9 ± 4,4	82,7 ± 1,21
	+ 6	67,4 ± 3,54	47,2 ± 6,03	115,8 ± 4,28	67,5 ± 12,5
18	+ 1	100,4 ± 1,43	86,3 ± 1,89	110,6 ± 2,28	92,7 ± 3,29
	+ 2	88,5 ± 1,94	67,6 ± 4,01	122,3 ± 1,12	90,2 ± 2,71
	+ 3	78,7 ± 7,74	69,2 ± 9,6	105,2 ± 4,3	84,7 ± 4,31
	+ 4	78,1 ± 4,05	54,3 ± 2,69	98,1 ± 4,16	68,3 ± 1,04
	+ 5	69,7 ± 4,68	50,3 ± 4,01	82,2 ± 3	59,4 ± 1,21
	+ 6	60,2 ± 8,2	45 ± 11,59	73,56 ± 5,3	48,3 ± 5,41

Source : MNHN, Paris

not sufficient. The interactions of the dental cells with the substratum are also important. These interactions appear to be more physiological with semi-solid medium than with Millipore filters.

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TABLE 4. Comparisons of mitotic indices of dental cells of mouse first lower molars growing *in vitro* and *in vivo*. A = ameloblasts; O = odontoblasts; PA = preameloblasts; PO = preodontoblasts. +, —: the mitotic indices *in vitro* are significantly higher or lower than the corresponding indices *in vivo*; =: no significant differences exist.

Stage	Days in culture	PO	PO + O	PA	PA + A
15	+ 1	= 16	= 16	— 16	— 16
	+ 2	= 17	= 17	— 17	— 17
	+ 3	= 18	= 18	= 18	= 18
	+ 4	+ 19	= 19	— 19	— 19
	+ 5	+ 20	+ 20	= 20	+ 20
	+ 6	+ 21	+ 21	+ 21	+ 21
16	+ 1	— 17	— 17	— 17	—17
	+ 2	— 18	— 18	= 18	= 18
	+ 3	= 19	= 19	+ 19	+ 19
	+ 4	+ 20	+ 20	+ 20	+20
	+ 5	+ 21	+ 21	+ 21	+21
17	+ 1	— 18	— 18	— 18	= 18
	+ 2	— 19	— 19	= 19	= 19
	+ 3	+ 20	+ 20	+ 20	+20
	+ 4	+ 21	+ 21	+ 21	+21
18	+ 1	— 19	— 19	— 19	—19
	+ 2	= 20	+ 20	— 20	+20
	+ 3	= 21	+ 21	— 21	+21

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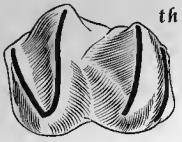
EVOLUTION OF DENTAL TISSUES



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Données Ultrastructurales sur la Ganoïne du Dermosquelette des Actinoptérygiens Primitifs

F. J. MEUNIER, M. GAYET, J. GÉRAUDIE, J.-Y. SIRE & L. ZYLBERBERG

ABSTRACT

Structural (light microscopy of ground sections) and ultrastructural comparative studies using scanning and transmission electronic microscopes on several parts of the dermal skeleton in Polypteridae and in Lepisosteidae on the one hand, and an experimental study of the regeneration of scales in *Calamoichthys calabaricus* and *Atractosteus tropicus* on the other, have permitted an understanding of the ontogenetic origin of the ganoine. The direct intervention of the epidermis in the production of the ganoine indicates that the latter is a true enamel. In another respect, the upper surface of the ganoid scales in living and fossil fishes always shows numerous tubercles, the size and density of which seem to be diagnostic characters at the generic and, sometimes, at the specific level. The ganoine of all the dermoskeletal elements with odontodes is separated from the epidermis by a special organic layer which may play an important mechanical role.

RÉSUMÉ

Des études comparatives structurales (microscopie photonique sur lames minces) et ultrastructurales (MET et MEB), sur divers éléments du dermosquelette de Polypteridae et de Lepisosteidae actuels et fossiles, d'une part, et une étude expérimentale de la régénération des écailles chez *Calamoichthys calabaricus* et *Atractosteus tropicus*, d'autre part, ont permis de préciser l'origine ontogénétique de la ganoïne. L'intervention directe de l'épiderme dans la production de la ganoïne permet d'interpréter cette dernière comme un émail vrai. Par ailleurs, la surface des écailles ganoïdes des poissons actuels et fossiles présente des petits tubercules dont la taille et la densité semblent être des caractéristiques diagnostiques au niveau générique et même, parfois, au niveau spécifique. La ganoïne de tous les éléments dermosquelettiques présentant des odontodes est séparée de l'épiderme par une couche organique particulière qui pourrait jouer un rôle mécanique important.

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Introduction

Les ouvrages spécialisés donnent en général des définitions simples et précises des différents types de tissus squelettiques des Vertébrés supérieurs et tout particulièrement des Mammifères pour lesquels des confusions d'interprétation semblent peu probables. Il en va tout autrement pour les Ostéichthyens, qu'il s'agisse des tissus osseux et de leurs dérivés formant un large continuum de structures (Meunier, 1983) ou encore des tissus dentaires pour lesquels de nombreuses variétés ont été décrites (Ørvig, 1967 ; Poole, 1967 ; Peyer, 1968).

En ce qui concerne les formations dentaires, il est remarquable de constater qu'après plus d'un siécle et demi de recherches, la question de l'origine de la couche hyperminéralisée la plus externe des dents et des odontodes [1] des Ostéichthyens, n'est toujours pas résolue (Hertwig, 1879 ; Goodrich, 1907 ; Kerr, 1952 ; Ørvig, 1967 ; Moss, 1968a, b ; Shellis & Miles, 1974, 1976 ; Meinke, 1982 ; Meinke & Thomson, 1983 ; Zylberberg *et al.*, 1985 ; Sire *et al.*, 1986). Cette incertitude résulte :

— des méthodes d'observations dans l'ensemble disparates compte tenu des diversités structurales ;

— du polymorphisme réel des structures dentaires, reflet de la grande diversification des lignées d'Ostéichthyens ;

— des schémas conceptuels dérivés directement de l'étude des Mammifères (quand ce n'est pas de l'Homme), souvent trop restrictifs dés que l'on aborde le monde des Vertébrés inférieurs et tout spécialement celui des Ostéichthyens.

Méthodologie

Dans le cadre d'une analyse comparée des éléments constituant le dermosquelette des Ostéichthyens fossiles et actuels, nous avons entrepris une étude de la couche superficielle hyperminéralisée des écailles ganoïdes : la ganoïne (Goodrich, 1907). Cette étude est fondée sur l'utilisation conjointe de techniques de microscopie photonique (lumière naturelle et lumière polarisée sur lames minces, microradiographie) et de microscopie électronique (MEB et MET). En combinant ces divers moyens d'investigation sur un abondant matériel fossile et actuel, nous avons essayé de préciser la structure de la ganoïne, ses relations avec les divers tissus voisins et la nature des cellules qui participent à sa formation.

Nous avons étudié :

— La morphologie de la surface (MEB) de la ganoïne ainsi que sa structure (lames minces) sur des écailles de diverses espèces du genre *Lepidotes* (Jurassique — Crétacé), des genres *Leptsosteus* et *Atractosteus* (Crétacé — Actuel), des genres *Polypterus* et *Calamoichthys* (sub-Actuel — Actuel), ainsi que quelques Paléonisciformes Paramblypteridae du Carbonifère et du Permien et un Halécomorphe du genre *Aphanepygus* (Cénomanien) ;

— L'ultrastructure (MET) de la ganoïne sur les écailles d'espéces actuelles : *Polypterus senegalus* Cuvier, 1829, *Calamoichthys calabaricus* (Smith, 1866) et *Atractosteus tropicus* Gill, 1863 ;

— Le rôle des différents types cellulaires (cellules épidermiques et cellules dermiques) dans la formation de la ganoïne au cours de la régénération expérimentale des écailles de *C. calabaricus* et *A. tropicus*.

A titre comparatif nous avons également fait un certain nombre d'observations avec les mêmes techniques sur d'autres pièces du dermosquelette porteuses d'odontodes comme les gulaires, les rayons épineux des pinnules dorsales, les « organes en V » des nageoires pectorales et les lépidotriches de *C. calabaricus* et *P. senegalus*.

Résultats-Discussion

Décrite pour la première fois par Williamson (1849), la ganoïne a reçu son nom de Goodrich

1 Nous appellerons « dent » toute formation dentaire localisée dans la cavité buccale et post-buccale (ou pharyngienne) et « odontode » toute formation dentaire associée au dermosquelette. Avec Ørvig (1977) nous admettrons que dents et odontodes sont des formations homologues.

Source : MNHN, Paris

(1907). C'est une substance hyperminéralisée (revue dans Ørvig, 1967 ; Meunier *et al.*, 1978 ; Meunier, 1980 ; Meinke, 1982) qui recouvre tout ou partie des écailles des Actinoptérygiens primitifs (Goodrich, 1907 ; Aldinger, 1937 ; Ørvig, 1967 ; Schultze, 1966, 1977). La trame minérale est constituée de cristallites de phosphate de calcium (Ermin *et al.*, 1971 ; Meinke *et al.*, 1979 ; Meinke & Thomson, 1983) fixés sur une trame organique pauvre et dépourvue de fibrilles de collagène (Sire *et al.*, 1986). Le grand axe des cristallites est orthogonal à la surface de l'écaille (Ørvig, 1967 ; Ermin *et al.*, 1971 ; Sire *et al.*, 1986). Sur les écailles, la ganoïne est pluristratifiée (Goodrich, 1907 ; Kerr, 1952 ; *inter alia*) alors que sur les odontodes des gulaires ou des rayons des pinnules des Polypteridae, elle est soit unistratifiée, soit á recouvrement partiel (Meunier, 1980 ; Meinke, 1982).

Observée au MEB, la surface de la ganoïne présente des reliefs en forme de tubercules arrondis, régulièrement espacés (Gayet & Meunier, 1986). Déjà observés sur les écailles de *Polypterus* par Ermin *et al.* (1971), ces tubercules sont présents sur les écailles de *Lepisosteus* (Fig. 1) et d'*Atractosteus* tant fossiles qu'actuels, de *Calamoichthys* (Fig. 2), de *Lepidotes* et d'*Aphanepygus*. Des tubercules sont également visibles chez les Paléoniscides comme l'avait déjà signalé Schultze (1977). D'ores et déjà, quelques résultats préliminaires peuvent être annoncés (Gayet & Meunier, 1986) :

— les tubercules sont des reliefs pleins et non de simples replis de la surface externe (en vue interne la ganoïne présente une surface parfaitement lisse) ;

— la taille et la densité de ces tubercules varient d'un genre — et même d'une espèce — á l'autre, ce qui semble pouvoir être un critère de détermination.

Ces tubercules sont caractéristiques de la ganoïne puisque présents de manière constante á la surface de la ganoïne unistratifiée des odontodes des gulaires (Fig. 3), des lépidotriches de la nageoire caudale (Fig. 4) et des rayons des pinnules chez les Polypteridae comme á la surface des éléments dermiques des Lepisosteidae. Ces tubercules pourraient avoir une fonction mécanique. En effet, sur les écailles par exemple, la ganoïne est recouverte par l'épiderme. Aucune structure fibreuse permettant un accrochage réciproque de la ganoïne et de la couche basale de l'épiderme n'a jamais été décrite, contrairement á ce qui est connu sur les écailles élasmoïdes (Junqueira *et al.*, 1970 ; Zylberberg & Meunier, 1981 ; Sire, 1985). En revanche, il existe toujours, á la place de la membrane basale entre la ganoïne et l'épiderme, une couche organique particulièrement bien structurée, la « couche intermédiaire » (Zylberberg *et al.*, 1985) qui assure une véritable jonction entre les deux tissus ; l'ensemble «tubercules-couche intermédiaire » pourrait ainsi assurer le rôle d'une « structure antidérapante » (ou d'amortisseur comme cela existe dans la peau des dauphins ; Kramer, 1965 *in* Burdak, 1979) minimisant le glissement de l'épiderme sur la ganoïne lors de l'écoulement de l'eau sur le tégument pendant la nage du poisson (Burdak, 1979). Cette couche intermédiaire se retrouve sur les divers odontodes du dermosquelette des Polypteridae (Zylberberg *et al.*, 1985), ainsi que sur les écailles d'*Atractosteus tropicus* (Fig. 5).

Chez *C. calabaricus*, l'ablation partielle ou totale d'une écaille entraîne des processus de régénération qui conduisent á la formation d'une nouvelle écaille de structure très voisine, sinon identique, á celle d'une écaille témoin, avec notamment une couche de ganoïne (Sire *et al.*, 1986). Il est donc possible, de cette façon, d'observer les différentes étapes de l'histomorphogénèse de la ganoïne.

L'apparition de la ganoïne est toujours précédée de la formation de la couche profonde d'os, puis de celle de dentine, plus superficielle. Les odontoblastes responsables de la dentinogénèse « s'écartent » et laissent la place, á la surface de l'écaille, aux cellules de la couche basale de l'épiderme qui établissent un contact direct avec la dentine (Fig. 6). Ces cellules épidermiques déposent une substance organique, la préganoïne (Fig. 6), qui se minéralise ensuite progressivement sur toute son épaisseur pour devenir la ganoïne (Fig. 10). Cette dernière présente á sa surface des tubercules de taille et de densité très voisines de ceux d'une écaille normale (Fig. 2). En même temps que la minéralisation de la préganoïne s'intensifie, une couche intermédiaire se met en place entre la ganoïne et l'épiderme.

Chez *A. tropicus*, les écailles régénérent selon des processus très semblables á ceux décrits chez *C. calabaricus*. Cependant, l'épiderme vient directement au contact de l'os (Fig. 7) puisque la

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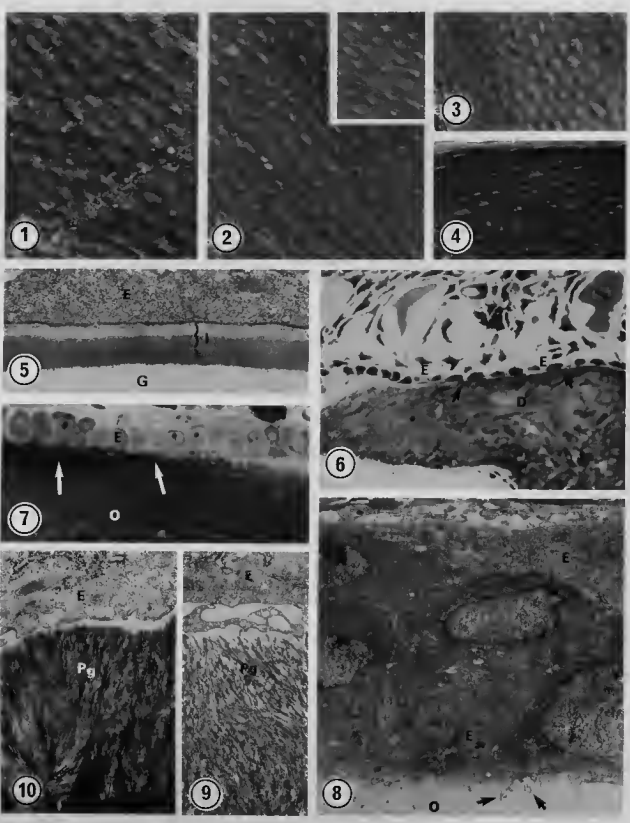

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dentine est inexistante sur les écailles des Lepisosteidae (Goodrich, 1907 ; Kerr, 1952 ; Meunier *et al.*, 1978). Ces cellules épidermiques secrètent ensuite la préganoïne (Fig. 9) qui se minéralise pour donner la ganoïne.

L'épiderme intervient donc directement dans la formation de la ganoïne des écailles régénérées. Celle-ci, par ses caractéristiques morphologiques (hyperminéralisation d'une trame organique dépourvue de collagène fibrillaire, cristallites orientés perpendiculairement à la surface de l'écaille) et ontogénétiques (dépôt d'origine épidermique suivant la formation de dentine), peut donc être considérée comme un émail vrai (voir les définitions dans Peyer, 1968, Shellis & Miles, 1976 ; Meinke & Thomson, 1983 ; *inter alia*), même en l'absence de données sur la nature des protéines (y-a-t-il ou non des amélogénines et des énamélines ?) qui constituent la trame organique, et non comme un émailoïde [2] (ou substance adamantoïde). Les ressemblances étroites existant entre ganoïne régénérée et ganoïne normale d'une part, et entre l'ontogénèse des écailles (Daget, 1950 ; Kerr, 1952 ; Meinke, 1982) et leur régénération (Sire *et al.*, 1987) d'autre part, nous incitent à considérer que la ganoïne non régénérée chez les Polypteridae et les Lepisosteidae est également un émail dont l'une des particularités est d'être stratifié.

Conclusion

D'une façon générale, sans vouloir rejeter l'existence d'une intervention dermique, dans le cadre d'interactions avec l'épiderme, lors de la mise en place des différentes couches de l'écaille ganoïde, nos observations montrent que la ganoïne, production épidermique, est bien un émail chez tous les Actinoptérygiens primitifs actuels. Cette conclusion serait également valable pour les Paléoniscides et les Holostéens fossiles si l'on considère la pérennité des caractéristiques morphologiques et structurales de la ganoïne entre formes fossiles et actuelles.

2 Terme utilisé par Kerebel & Daculsi, 1975.

Figs. 1 à 4 — Observation au MEB de la surface de la ganoïne :

Fig. 1. — Écaille de *Lepisosteus cuneatus* ; Éocène, Green River, USA. (× 700).

Fig. 2. — Écaille de *Calamoichthys calabaricus* ; dans l'encart, une écaille régénérée. (× 700).

Fig. 3. — Odontode d'une plaque gulaire de *Polypterus senegalus*. (× 700).

Fig. 4. — Odontode d'un lépidotriche de la nageoire caudale de *P. senegalus*. (× 370).

Fig. 5. — Coupe ultrafine d'une écaille d'*Atractosteus tropicus* au niveau de la couche intermédiaire (I), zone de transition entre l'épiderme (E) et la ganoïne (G), disparue après décalcification. Noter l'aspect lamellieux de la partie la plus externe de la couche intermédiaire (décalcification EDTA). (× 26 000).

Fig. 6. — Coupe semi-fine d'une écaille en régénération depuis deux mois de *C. calabaricus*. Noter le contact (flèches) des cellules basales de l'épiderme (E) avec la dentine régénérée (D) (décalcification EDTA, rouge de ruthénium, bleu de toluidine). (× 400).

Fig. 7. — Coupe semi-fine d'une écaille en régénération depuis trois mois d'*A. tropicus*. Noter le contact des cellules basales de l'épiderme (E) avec l'os régénéré (O). Chez les Lepisosteidae il n'y a pas de dentine. Les premiers dépôts de préganoïne montrent une forte métachromasie (flèches) (décalcification EDTA, bleu de toluidine). (× 800).

Fig. 8. — Coupe ultra-fine dans la région superficielle d'une écaille en régénération depuis trois mois d'*A. tropicus*. Les cellules de la couche basale de l'épiderme (E) ont une forme cuboïdale. Leur plasmalemme basal est au contact des fibrilles de collagène de la couche osseuse (O) ; la membrane basale a disparu et des prolongements cytoplasmiques pénètrent dans l'ostéoïde (flèches). (× 6 600).

Fig. 9. — Coupe ultra-fine d'une écaille en régénération d'*A. tropicus* montrant la formation, par les cellules épidermiques (E), de la préganoïne (Pg) ; noter l'aspect fibreux de la trame. (× 13 000).

Fig. 10. — Coupe ultra-fine d'une écaille en régénération depuis deux mois de *C. calabaricus* montrant la minéralisation de la préganoïne (Pg) ; (E = épiderme). (× 26 000).

Source : MNHN, Paris

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The Nature and Significance of Enamel Tubules in Therapsids and Mammals

A. SAHNI & K. S. LESTER

ABSTRACT

There is currently a resurgence of interest in the analysis of enamel with a view to understanding more fully its evolution and, through this, its possible usefulness in an increased application to taxonomy. In this paper, enamel tubules are presented as a structural feature of significance as they appear or have been reported in reptiles (modern and extinct), most multituberculates, all marsupials except the wombat and as a normally vestigial element in many placentals. The enamel of sectioned and whole teeth from therapsids, multituberculates and marsupials is specifically illustrated by scanning electron microscopy in the context of this historical review.

The accumulated evidence suggests that the present-day characteristics of eutherian enamels, including enamel tubules, were established at least over 100 million years ago. The indications are also that the feature of enamel tubules, carefully quantified and reviewed, is of considerable potential taxonomic value. The desirability of expanding our present knowledge of the structure, distribution and function of enamel tubules is clear as is the need to move towards an improved sampling and a more quantitative analysis of this in conjunction with other significant enamel characters.

RÉSUMÉ

On assiste actuellement à un renouveau d'intérêt pour l'analyse de l'émail, dans l'espoir de mieux comprendre son évolution et, à travers elle, de rechercher son éventuelle utilité dans la taxonomie. Dans cet article, les tubules de l'émail sont présentés comme un trait structural significatif ; ils existent en effet ou ont été signalés chez les reptiles (modernes et éteints), la plupart des multituberculés, tous les marsupiaux sauf le wombat, et, en temps qu'élément vestigial, chez de nombreux placentaires. L'émail de dents entières et sectionnées de thérapsides, multituberculés et marsupiaux est figuré au SEM dans le contexte de cet historique.

Les faits accumulés suggèrent que les caractères actuels de l'émail des Euthériens, y compris les tubules de l'émail, ont été établis il y a au moins 100 millions d'années. Il apparaît aussi que le caractère « tubules de l'émail », soigneusement quantifié et revu, présente une grande valeur taxonomique potentielle. Il est clair qu'il convient d'étendre notre connaissance actuelle de la structure, de la répartition et de la fonction des tubules de l'émail, et aussi d'améliorer notre échantillonnage et de réaliser une analyse plus quantitative de ce dernier, conjointement aux autres caractères significatifs de l'émail.

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Source : MNHN, Paris

Introduction

The last two decades have witnessed a resurgence of interest in the subject of the evolution of enamel. This attention reflects the realization that fossil mineralized tissue rarely undergoes substantive structural, as opposed to chemical, modification with time and that the structural diversity in extinct genera affords an added, essential dimension to our understanding of the enamels of living vertebrates. Concomitant with this interest, the advancement of instrument technology (more especially in electron microscopy and microradiography) and the availability of better documented lineages in the fossil record have contributed considerably to an improved understanding and appreciation of the subject. Whilst the theme of enamel evolution is of concern to various life and earth scientists, the subject has not yet been tackled on a multidisciplinary basis. Hence the results of various studies, although meaningful in their own right, lack integration. Of the many mammals available for investigation, evolutionary analysis of enamel structure has been carried out in the following groups: primates (Gantt, 1980; Boyde & Martin, 1982), rodents (Korvenkontio, 1934; Wahlert, 1968; von Koenigswald, 1980; Sahni, 1980, 1984, 1985), canids (Reif, 1974), proboscideans (Kozawa, 1978), cetaceans (Ishiyama, 1984; Sahni, 1981), rhinoceroses and other lophodont ungulates (Fortelius, 1984), monotremes (Lester & Archer, 1986), and multituberculates (Moss, 1969; Fosse *et al.*, 1973, 1978, 1985; Sahni, 1979; Carlson & Krause, 1982, 1985).

Tubule formation and development have remained a source of controversy since the earliest report by Tomes (1850). Enamel tubules constitute one of the important characteristics of the enamels of extinct and extant marsupials as well as of a number of primitive mammalian groups and reptiles. When viewed in evolutionary perspective, the presence of enamel tubules assumes especial significance as they appear to be a prominent feature of non-placental mammals (allotherians and metatherians). Most of the studies on fossil tubular enamel (Moss, 1969; Fosse *et al.*, 1973; Osborn & Hillman, 1979) have been interpreted in the light of the enamel of living marsupials — the latter being now fairly well established (for example, Boyde & Lester, 1967, 1984).

Prior to the 1970's the majority of the work on enamel tubules was accomplished with the light microscope. Tubules were considered a feature of enamel but secondary in importance to other characters: the pattern of cross-sectional outline of prisms; prism diameter; layering; prism decussation; enamel thickness and the striae of Retzius. So that although the presence of enamel tubules is very often mentioned in descriptions of enamel, the modern ultrastructural basis for these studies was established mainly on the work of Boyde (1964), Boyde & Lester (1967), Lester (1970) and Boyde & Lester (1984). While the ultrastructural basis for prism shape and pattern was determined in great measure by Boyde (1964), considerable controversy continues to surround the nature of the enamel tubules and particularly the mechanism by which they appear continuous with the dentinal tubules. In recent years, Lester (1970) and Boyde & Lester (1984) have proposed that the enamel tubules function as accessory channels to facilitate the flow of materials necessary to the maturation-mineralization process and that the continuity of tubules from the occlusal surface across the enamel-dentine junction to the dentine may serve to signal the need to produce secondary dentine. The absence of enamel tubules within a lineage generally characterized by tubular, prismatic enamel remains, however, a mystery. The classic example of this was observed over 150 years ago in the marsupial *Vombatus* (Tomes, 1849, 1850). Conversely, Ishiyama (1984) has recently recorded the presence of non-prismatic, tubular enamel in *Phoconoides* while other cetaceans, both recent and fossil, are known to possess prismatic, generally non-repetitively tubular enamels (Sahni, 1981).

This paper presents, both by description and review, the structure and distribution of tubules in enamel as a representative feature of reptilian and mammalian enamels.

Material and method

A. *Whole multituberculate teeth*

Non-specified multituberculate teeth, both whole and fragmented, were supplied by one co-author

Source : MNHN, Paris

(A.S.) to the other (K.S.L.). The teeth were air-polished™ (Boyde, 1984), lightly etched (0.5 % H_3PO_4 for 5 seconds) and after coating, the external surfaces (whole, worn and/or possibly damaged) were examined by scanning electron microscopy.

B. *Sectioned therapsid and multituberculate teeth*

The fossil specimens comprising traversodontid therapsids and multituberculates[1] were sectioned and treated with 2-3 % HNO_3 for etching times ranging from 8 to 20 seconds. After etching, the material was washed and cleaned in an ultrasonic vibrator prior to examination by scanning electron microscopy — this treatment helps remove salts which precipitate as a result of the acid reaction. The procedure of etching can be regarded in many ways as a necessary evil in that it helps to create a scannable micro-relief which reflects the internal geometry and orientation of the enamel apatite crystallite groups. Sometimes, however, etching causes the widening of incipient fractures in fossil material, the apparent enlargement of tubule diameters, and the build-up of precipitants along the margins of prisms.

In most of the fossil material studied, it was observed that enamel and dentinal tubules form casts of re-crystallized dolomitic calcite or siliceous material in chalcedonic form which preferentially stand out in relief after etching of the carbonate apatites of the enamel. The fact that natural casts commonly occur in the fossil specimens clearly indicates that the material inside the lumen of the tubules at the time of burial of the animal contained easily degradable organic material which allowed mineralizing solutions and clay-sized particles to enter the tubules in a fluid phase. This was probably accomplished through access to the pulp cavity via openings in the supporting mandibular and maxillary bone. From the pulp cavity, the ingressing solutions could travel through the dentinal tubules across the enamel-dentine junction to the inner part of the enamel.

Studies conducted on fossil dental material in the Vertebrate Palaeontological Laboratories, Geology Department, Chandigarh, demonstrate that post-mortem mineralizing solutions do not enter through the resistant, hard (usually non-prismatic), outer, thin layer of enamel unless the fossil tooth has been diagenetically altered and fractured (P. S. Suri, in preparation). The uniform diameter of the dentinal and enamel tubules and the smooth nature of the surface of the natural casts suggest that the infilling solutions were not at all viscous and were able to penetrate tubular spaces of less than 0.5 μm in diameter. The absence of well-branched tubular casts in the enamel, in contrast to the markedly branched tubules of the dentine (Figs. 8 and 9), is almost certainly not an artifact of preservation but rather indicative of the original histological condition. The branches of dentinal tubules (secondary and tertiary) have diameters of less than 0.2 μm.

C. *Australian marsupial teeth*

Adult teeth from dried skulls of the extant Australian marsupials : *Phascolarctos cinereus, Macropus rufus, Macropus rufogriseus, Rufous bettong* and *Wallabia bicolor*, were also prepared for examination by scanning electron microscopy[2]. Outer, functional surfaces were air-polished™ (Boyde, 1984), and, in some teeth, grooves were cut in various planes of the tooth with a 1 mm diameter, plain tungsten carbide high speed fissure bur. Phosphoric acid (1 % for 10 seconds) was used to reveal the prismatic structure. The exposed surfaces were carefully washed in distilled water, dehydrated through alcohols and gold coated prior to examination at 15kV in the SEM.

Results

A. *Whole multituberculate teeth*

Figs. 1 and 2 illustrate a facet on the occlusal surface of a multituberculate (*Mesodma*) molar.

1 The multituberculates used in the present work have been described earlier (Sahni, 1979).

2 These teeth were initially prepared and examined in collaboration with Prof. A. Boyde and many features of the enamel described elsewhere (Boyde & Lester, 1984).

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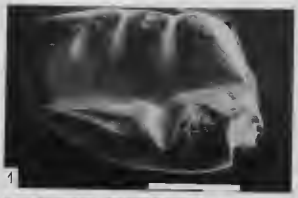

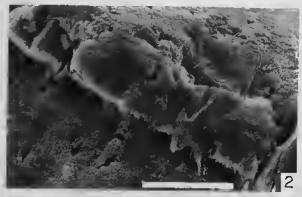

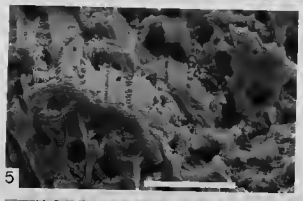

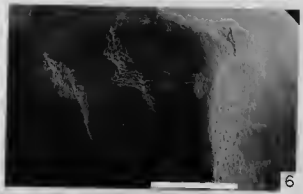

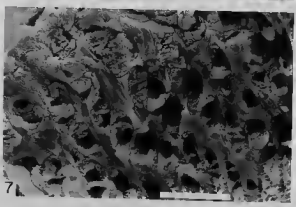

Source : MNHN, Paris

This was possibly a functional attrition facet and has exposed enamel, the enamel-dentine junction and the dentine. Enamel tubules cross the enamel-dentine junction continuous with dentinal tubules and pass through the thin enamel layer to reach its external surface. Crystallite groups in the enamel are not organized into domains in this particular region of the enamel coating although the "gigantoprisms" of Fosse *et al.* (1973) were evident where the enamel was thicker (Fig. 3).

In another (*Mesodma*) molar specimen (Fig. 4), was found a facet more probably resulting from damage rather than function (Figs. 4 and 5 locate, and Figs. 6 and 7 show details of, the tubular and prismatic structure). Tubules are located predominantly in the prisms (Fig. 6) and occasionally towards their boundary with the inter-row sheet. The prisms are arranged for the most part (especially the middle third) in a Pattern 2 packing pattern (Boyde, 1964) (Fig. 7) although Pattern 1 and a modified Pattern 3 are also found (Sahni, 1985). In this specimen, the tubules become increasingly less obvious and do not progress to the outer enamel surface (Fig. 7).

An incisor fragment with an exposed fractured dentine surface displayed multiple casts of highly branched odontoblast processes (Figs. 8 and 9).

B. *Sectioned therapsid and multituberculate teeth*

Traversodontid Cynodont :

These reptiles belong to the Therapsida, a group of mammal-like reptiles which are considered to be ancestral to the mammals. *Pachygenelus* enamel has been described as prismatic (Grine *et al.*, 1979) and is similar to that of the Indian traversodontid cynodont (Sahni, 1985). Other cynodonts, however, are described as non-prismatic (Moss, 1969; Grine, 1978; Osborn & Hillman, 1979). There is however some confusion and uncertainty at present concerning the definition and delineation of "pseudo-" and "pre-" prismatic enamels.

Enamel tubules in therapsids and primitive mammals were considered to act as "pain sensors" by Osborn & Hillman (1979). These authors attached considerable significance to the increase in tubular density amongst the therapsid-non/therian mammalian evolutionary lineages.

The specimens described here are represented by four complete, cuspate molars and a few fragments and were obtained from the Triassic of peninsular India in the Godavari-Pranhita Basin (Chatterjee *et al.*, 1969). As the teeth were recovered in an isolated condition, it is as yet not possible to assign precisely a generic name. The cynodonts described from the locality yielding

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Figs. 1-9 are scanning electron micrographs of whole or already fragmented (as recovered), air-polished, lightly etched, multituberculate teeth supplied by one co-author (A.S.) to the other (K.S.L.) for examination.

Figs. 1-3 are of the same specimen (*Mesodma*, lower left second molar — Cretaceous, Montana).

Fig. 1. — Whole tooth seen from the occlusal and showing flattened cusps, wear facets and localized areas where enamel has fractured away from the dentine. The area illustrated in Fig. 2 is located by the arrow. Bar = 1 μm.

Fig. 2. — Higher magnification of air-polished and lightly etched exposed enamel and dentine (see arrow in Fig. 1 for location). The enamel and dentinal tubules are continuous across the enamel-dentine junction and reach the outer enamel surface. The enamel here is not organized into prisms although it is elsewhere in the specimen. Bar = 10 μm.

Fig. 3. — A thicker area of enamel showing large diameter prisms and occasional tubules. Bar = 10 μm.

Figs. 4-7 are of the same specimen (*Mesodma*, upper right first molar — Cretaceous, Montana).

Fig. 4. — Whole tooth seen from the occlusal and showing flattened cusps, wear facets and localized areas where enamel has fractured away from the dentine. The area illustrated in Fig. 5 is located by the arrow. Bar = 1 μm.

Fig. 5. — Fractured prismatic enamel (air-polished and lightly etched) adjacent to a worn cusp with dentine exposed (for location see Fig. 4). The areas illustrated in Figs. 6 and 7 are located by the numbered arrows. Bar = 100 μm.

Fig. 6. — Higher magnification of area located in Fig. 5 showing tubule location to be predominantly within the prisms (at arrows). Bar = 10 μm.

Fig. 7. — Higher magnification of area located in Fig. 5 showing development of inter-row sheets, a Pattern 2 kind of prism packing, a non-prismatic surface layer and a relative absence of enamel tubules towards the outer enamel surface. Bar = 10 μm.

Figs. 8 and 9 are of the same fragmented incisor specimen and show "naturally occurring" odontoblastic tubule casts with significant multiple branching — the arrow in Fig. 8 locates the cast for Fig. 9. Bars = 10 μm and 1 μm respectively.

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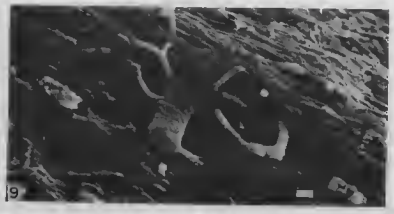

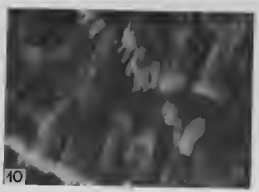

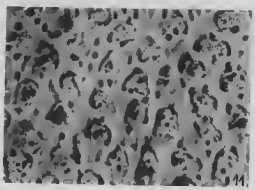

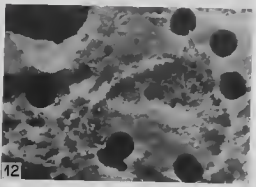

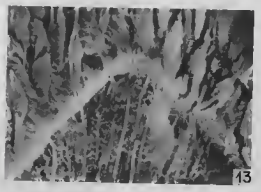

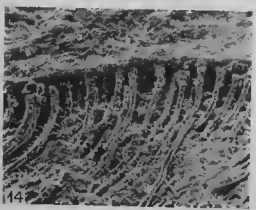

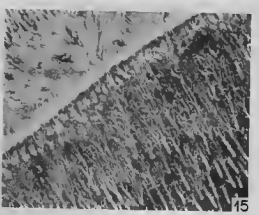

Source : MNHN, Paris

the isolated teeth include the genera *Wadiasaurus indicus* and *Rechnisaurus crystarhynchus*.

Suggestions of prismatic structure were found in some of the sections of the more highly etched teeth, but were not found to be a conspicuous or even continuous feature throughout the extent of the enamel thickness. Most of the specimens exhibited well defined incremental lines. Tubules are not represented here by natural casts but consist of tubular continuations from the dentine across the junction and into the enamel. In some of the sections studied, the tubules appear to follow a path parallel to the prisms (Fig. 10). The outer dentinal region appears to be differentiated into a 20 to 40 μm width band in which the longitudinally oriented dentinal tubules are transversely sectioned in the same plane. The enamel tubules are again oriented longitudinally and cuspally towards the outer surface.

MULTITUBERCULATES :

As far as is known, both the allotherians and metatherians had tubular enamel in the Late Cretaceous, the enamel of the eutherians on the other hand is non-tubular. Multituberculate enamel has been extensively studied in the last decade and forms the basis for most of the data on the enamel structure of non-placental, fossil mammals. Although not clearly stated by him, Carter (1922) would seem to be the first to have recognized that at least some multituberculates had large prisms. Moss (1969) considered multituberculate enamel to be non-prismatic but observed differences in the width of " bands " which correspond to the larger than normal (for placental) prisms in some multituberculates, later termed " gigantoprisms " by Fosse *et al.* (1973). It has recently been shown that the occurrence of gigantoprisms is restricted to only one of the two suborders, namely, the Taeniolabidoidea, the other suborder, the Ptilodontoidea, having the more normal eutherian prism diameter (Carlson & Krause, 1985). All workers (Moss, 1969; Fosse *et al.*, 1973; Sahni, 1979 and Carlson & Krause, 1982, 1985) are agreed that multituberculates have enamel tubules to varying degrees.

Data on the density and the distribution of enamel tubules are currently limited. According to Sahni (1979), tubular enamel was more common in the taeniolabidoids, with the highest density amongst the genera studied in *Catopsalis*. Transversely sectioned circular tubules are abundant in both the prismatic and interprismatic regions of *Catopsalis* (Fig. 11). In all the specimens studied, the orientation of the tubules remained essentially parallel to the course of the prisms. In all the transversely sectioned prisms, the enamel tubules were also transversely sectioned and possessed circular outlines (Fig. 12). In none of the specimens studied were longitudinally sectioned tubules observed cutting across the transversely sectioned outlines of the prisms. This is rather surprising because wherever natural casts have been preserved, their extensions show that the tubules cut across the width of several prisms. On the other hand, in longitudinal sections of the enamel, the course of the tubules can be traced both in the inter-prismatic and prismatic regions.

In *Mesodma* as in other multituberculates, the relationship of enamel and dentinal tubules

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FIG. 9. — Voir page 89.

FIG. 10. — Traversodontid cynodont, longitudinal section of cuspate tooth showing dentine at base. Enamel tubules oriented normal to the enamel-dentine junction. Prism structure poorly organized. × 1 400 approx.

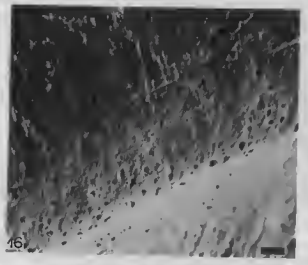
FIGS. 11 and 12. — *Catopsalis*, occlusal surface of second lower molar showing abundant enamel tubules occurring in both the prismatic and inter-prismatic regions. The distribution of tubules, especially where they are closely clustered may indicate branching (Fig. 11). Enlarged view of single prism showing tubules. Note the circular cross-section of the inter-prismatic tubules. Fig. 11 = × 615 approx. Fig. 12 = × 4 260 approx.

FIG. 13. — *Mesodma*, longitudinal section of fourth upper premolar showing enamel-dentine junction near apex of the crown. Enamel tubules are clearly continuations of the dentinal tubules. The tubules exhibit a pronounced bending while entering the enamel and are oriented normal to the enamel-dentine junction along the lateral margins. × 800.

FIG. 14. — *Stygimys*, lower fourth premolar showing dentinal tubules intersecting the enamel-dentine junction. In general, the tubules are oriented parallel to one another and do not appear to extend into the enamel. × 800.

FIG. 15. — *Birbalomys woodi*, transverse section of incisor of a ctenodactylid rodent from the Middle Eocene of India showing highly branched dentinal tubules. No enamel tubules have yet been observed in this and other eutherian taxa from the Cretaceous or the Early Tertiary. × 460 approx.

Source : MNHN, Paris



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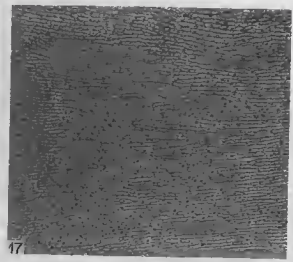

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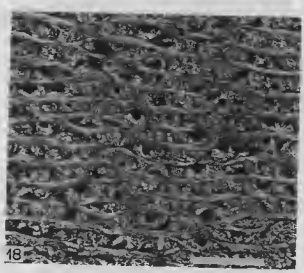

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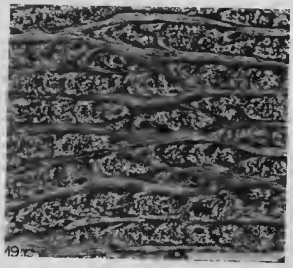

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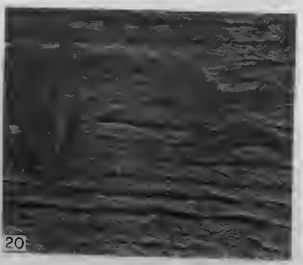

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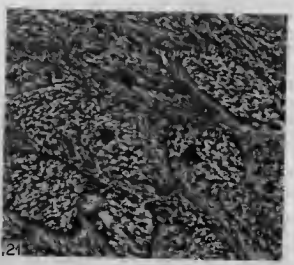

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Source : MNHN, Paris

indicates continuity of these structures (Carter, 1922; Moss, 1969; Fosse *et al.*, 1973; Osborn & Hillman, 1979; Sahni, 1979). Natural casts of the enamel tubules can be seen bending and following the course of the prisms. Tubules at the apex of the transversely sectioned upper fourth premolar of *Mesodma* are oriented parallel to the dentinal tubules. However, on the lateral margins which are steeply inclined, the tubules are deflected to the labial and the lingual sides. In most cases, the most pronounced bending of the dentinal tubules is near the enamel-dentine junction (Fig. 13). In their study of *Mesodma* enamel, Carlson & Krause (1985, fig. 12A) report the absence of tubules.

In *Stygimys*, the dentinal tubules entering the enamel-dentine junction are in parallel and of uniform thickness (Fig. 14). Enamel tubules are rare to absent and this observation is also supported by Carlson & Krause (1985).

In eutherian mammals (*Cimolestes, Gypsonictops* from the Late Cretaceous, and the rodent *Birbalomys* from the Middle Eocene of India), natural casts of tubules have been observed in the dentine. In most cases, these are profusely branched (Fig. 15). However, in none of these instances has the extension of these tubules been observed in the enamel. The evidence suggests that the present-day characteristics of eutherian enamels with regard to the absence of enamel tubules as a significant feature were established at least over 100 million years ago, if not earlier.

C. *Marsupial teeth*

It is important to appreciate that marsupial enamel tubules are not merely an internal feature but for whatever function they may perform are in many species made available either to the natural, formed enamel surface (Boyde & Lester, 1984) or to functional attrition facets. Fig. 16 shows typically dense and large tubules at a naturally occurring, functionally exposed enamel-dentine junction in *Wallabia bicolor* treated only with air-polishing ™.

Tubule size, distribution, location and frequency vary in different parts of one tooth, different teeth of the same species and comparable teeth of different species of marsupial. It is our intention to try to characterize these species differences. Examples of this in three species are shown in Figs. 9 to 20. *Rufous bettong* has a high frequency of tubule occurrence characteristically in well-ordered enamel and predominantly located at mid-prism (Fig. 17). *Macropus rufus* has a similarly high frequency but of larger tubules and near the enamel-dentine junction (*cf.* Figs. 18, 19); the tubules are located at the junction of prism and inter-row sheet. *Phascolarctos cinereus* possesses small tubules located at mid-prism, numerous at the enamel-dentine junction but becoming less so towards the outer enamel (Fig. 20).

Characteristically, tubules are very much easier to identify in transverse section (Figs. 16-20). In longitudinal section, they are usually identified with confidence only when located in the middle

FIGS. 16-21 are scanning electron micrographs of whole and prepared surfaces of dried mature Australian marsupial teeth. These specimens were initially prepared and examined in collaboration with Professor A. Boyde (*see* Boyde & Lester, 1984).

FIG. 16. — Naturally worn facet of occlusal surface of a *Wallabia bicolor* molar showing numerous exposed tubules at the level of the enamel-dentine junction. The frequency of tubule occurrence decreases away from the junction (to top left). The dentine, being softer and more easily worn, is out of focus to the bottom right. Bar = 10 μm.

FIG. 17. — *Rufous bettong* molar in which a 1 mm deep groove was cut on the buccal surface in the longitudinal axis of the tooth and air-polished only. The enamel shows a very high frequency of tubules although never more than one per prism. The tubules are located within the prism and often adjacent to the prism border towards the inter-row sheet. Bar = 100 μm.

FIGS. 18 and 19. — *Macropus rufus* molar (cut, air-polished and etched) showing enamel near the enamel-dentine junction, where the tubules are both larger (up to 2 μm in diameter) and more numerous (Fig. 12), and towards the outer enamel surface (Fig. 13). Again the tubules occur most often within the prism but with the inter-row sheet contributing significantly to their outline. Bars = 10 μm.

FIG. 20. — *Phascolarctos cinereus* molar enamel showing small tubules located towards the junction of prism either with prism or with inter-row sheet. Bar = 1 μm.

FIG. 21. — *Rufous bettong* molar with a cut, air-polished enamel surface showing a longitudinal section of tubule at the prism. Longitudinally sectioned tubules are difficult to identify with confidence (unless located at mid-prism) but easier where the enamel is air-polished only and not etched. Bar = 10 μm.

Source : MNHN, Paris

of a prism. When located at the junction of a prism with either another prism (Fig. 21) or inter-row sheet, there is always the possibility to be considered that the tubule is merely a deficiency in the prepared surface as a result of some localized damage in preparation (cutting or etching) exaggerating a boundary plane between crystallite domains.

Discussion

Historical Perspective and Geological Record

Enamel tubules as currently known are found in certain living reptiles (the iguanid lizard, *Uromastyx*) as demonstrated by Cooper & Poole (1973); in extinct reptiles (Therapsida) as reported by Osborn & Hillman (1979) and Sahni (1984, 1985); in most multituberculates (possibly more so in taeniolabidoids); in all known marsupials except *Vombatus*; and in a variety of other non-placentals. In placental mammals, their significant presence in mature enamels is usually exceptional, as for instance in *Phoconoides* (Ishiyama, 1984). Enamel tubules thus represent a minor, normally vestigial element in eutherian enamels. Their presence has been recorded in primates, e.g., Lemuroidea (Carter, 1922) and humans (Boyde & Lester, 1967), suids (Kozawa *et al*, 1981), insectivores and rodents (Tomes, 1849), chiropterans (Loher, 1929; Boyde, 1964; Boyde & Lester, 1967); cetaceans (Ishiyama, 1984) including possibly the dolphins (Boyde & Lester, 1967), and in the hyraces.

In discussing the probable stages in the transition of reptilian to mammalian enamels, Poole (1967) considered the derivation of the mammalian structural grade a relatively simple process, but concluded that tubular enamels present in the majority of marsupials and some placentals must be a later specialization of the simpler, prismatic type. According to Poole (1971), tubular enamel possesses both prisms and tubules, the latter arising at the enamel-dentine junction and confined to tbe inter-prismatic phase. The presence of prisms suggested that tubular enamel was related to the more normal mammalian type but " ... the tubules, the peculiar optical properties and the extremely high organic content, all point to a specialized type of prismatic enamel ".

Sprawson (1930) had earlier described tubules as inter-prismatic with a tendency to disappear with advancing age and wear of teeth. Boyde & Lester (1984) would disagree with this having observed exposed tubules in large numbers at functional, attritional facets of mature teeth in a number of marsupial species.

The contribution by Moss (1969) high lighted the diversity in therapsids and primitive mammals for the first time. Some of his observations on enamel microstructure carried out by light microscopy have been shown to be ill-founded on the basis of later SEM studies (Fosse *et al*., 1973). However, the large sample that he studied still forms the foundation for most of the later works. It is possible that many of his observations on the presence of enamel tubules may have been based on hairline fractures unrelated to the course of the tubules themselves as was discussed by Osborn & Hillman (1979). Moss (1969) described tubules in the therapsid *Sesamodon brownii* (Family Bauriidae) from the Early Triassic of South Africa. He showed that multituberculates had tubular enamel starting from the Late Jurassic plagiaulacids, including Campanian multituberculates from Wyoming and the well known North American Cretaceous genera, *Meniscoessus* and *Cimolodon*. He also demonstrated that enamel tubules persisted in the Palaeocene and Eocene members of the Multituberculata.

Moss (1969) was amongst the first to document the presence of enamel tubules in fossil marsupials and referred to the role of these structures in the change to the positive birefringence of recent marsupial enamels. He saw the difference as a result of the tubular spaces in the fossil enamels being filled with intrusive material imparting a negative birefringence to the massed apatite crystallites. He demonstrated that, except for a Campanian marsupial in which the tubular spaces were sparse, all other Late Cretaceous North American marsupials (*Pediomys*, *Alphadon*, and indeterminate didelphids) had tubular enamel. He noted that in *Pediomys*, the cervical enamel was totally free of tubules and concluded overall that tubular enamel occurs independently of a prismatic or non-prismatic structure (Moss, 1969).

Fosse and his co-workers (Fosse & Holmbakken, 1971, Fosse *et al*., 1973) concluded on the basis of their study of recent marsupials and

Source : MNHN, Paris

multituberculates, that tubules in marsupial enamels contain an acid-resistant residue. In multituberculates, dentinal tubules are branched while in the enamel they are " smooth "; the diameter of tubules both in the dentine and enamel are the same; and the enamel tubules could not be traced beyond one-third of the enamel thickness from the enamel-dentine junction. The other major conclusions were that tubules follow the course of the prisms over only a short distance and that each tubule could be observed crossing several individual prisms. Fosse *et al.* (1973) supported the contention of Moss (1969) that enamel tubules follow a zig-zag or spiral " centrifugal " course and considered enamel tubules as extensions of the dentinal tubules found both in the prismatic and inter-prismatic phases. According to these authors, enamel tubules could not possibly be the products of a single ameloblast although they must have contained the cytoplasmic processes of these secretory cells.

Cooper & Poole (1973) have shown the presence of Pattern 1 prisms in the lizard *Uromastyx* together with enamel tubules both by optical and scanning electron microscopy. The enamel tubules are commonly seen near the enamel-dentine junction. According to these authors, the dentinal tubules are markedly branched while peritubular dentine probably does not exist.

Osborn & Hillman (1979) re-studied most of the genera earlier investigated by Moss (1969) and included a number of different taxa (particularly those of therapsids) in their analysis. They attempted to find reasons for apparent discrepancies in the recording of enamel tubules based on light microscopy and scanning electron microscopy. They suggested that transverse sections of enamel were as important as longitudinal sections in determining the existence of enamel tubules in thin sections. They observed a definite increase in density of enamel tubules from *Thrinaxodon* to *Diademodon* and lastly to *Massetognathus*. In contrast to the findings of Moss (1969), they found that tubules were present in *Pediomys* (Marsupial, Late Cretaceous) and were located on the prism sheath. They further reported tubules in two Late Cretaceous placentals (*Procerberus* and *Protungulatum*). If true, this would represent the earliest record of enamel tubules in eutherians. However, SEM studies of *Protungulatum* (Sahni, 1979) have failed to reveal any tubular structure in the enamel. Osborn & Hillman (1979) found that the fossil marsupial *Alphadon* had a structure similar to that of the Recent *Didelphis* with tubular structures on the " prism sheaths ". In multituberculates, the prisms were found to average 7 μm and the tubules " weaved in and out of prisms ".

In other taxa critical for understanding the evolutionary significance of enamel tubules, the presence or absence of tubules has not been specifically mentioned. Thus Grine (1978) and Grine *et al.* (1979) do not report enamel tubules in *Tritylodon* and *Diademodon* (Therapsida) which have non-prismatic enamel. Again, in *Pachygenelus* which has a prismatic pattern, no mention is made of their presence. In the " preprismatic " enamel of the Late Triassic Kuehneotheriidae and Haramiyidae, which are believed to be ancestral to the multituberculates, there is no known record of enamel tubules (Frank *et al.*, 1984, Sigogneau-Russell *et al.*, 1985). Fosse *et al.* (1985) reported some enamel tubules in the enamels of plagiaulacoid and docodont taxa. The density of these enamel tubules was greater in the genera *Chulsanbaatar, Kryptobaatar* and *Stygimys*.

Sahni (1979) illustrated the existence of tubular enamels in a number of multituberculates both in the prismatic and the inter-prismatic phases. Natural casts of tubules clearly demonstrated the continuity of dentinal tubules with those of the enamel across the enamel-dentine junction. In one specimen of *Catopsalis*, a unique but characteristic pattern for the distribution of enamel tubules was observed: tubules were restricted to the inter-prismatic layer near the enamel-dentine junction; further cuspally was a zone showing prismatic and inter-prismatic tubules; and finally tubules showed confinement within the prisms. Such a distribution of tubules in enamel was not found however to apply to other specimens of *Catopsalis* studied nor to multituberculates in general.

Lester (1970) described by transmission electron microscopy the origin and nature of the contents of enamel tubules in developing teeth of the opossum *Didelphis marsupialis*. He found that the tubules contain cell processes (the " fibrils " of earlier workers) which are extensions of ameloblast cytoplasm originating at the mineralizing front of the enamel. Subsequently, Boyde & Lester (1984) studied the mature teeth of seven species and the developing teeth of five

Source : MNHN, Paris

species of Australian marsupial by transmission and scanning electron microscopy. They concluded that :

— enamel tubules are open spaces which may be embedded with methylmethacrylate;

— many enamel tubules are continuous with dentine tubules at the enamel-dentine junction and many are not, the details varying between species;

— the most frequent location of tubules is at prism border locations or in prism bodies;

— although not every prism has a tubule some have more than one;

— tubule locations can be related to tubular deficiencies opening at the developing enamel surface; and

— enamel tubules can be seen arriving at outer enamel surfaces but are more readily identified at worn occlusal surfaces.

Kozawa *et al.* (1981) have shown the presence of enamel tubules in developing pig enamel and a possible correlation with the tubular enamel reported in primitive fossil mammals. They observed the projection of tubules into the enamel arising from the Tomes' process. Cell organelles including coated vesicles were found in these projections and, in later developmental stages, calcium crystals were reported as deposited in these tubules.

In their comprehensive account of multituberculate enamel ultrastructure, Carlson & Krause (1985) have drawn attention to the distribution of enamel tubules in the various genera studied by them. They found (p. 17) that, in general, as the prism structure becomes better organized and regular, the number of enamel tubules (if these are at all present) reduces cuspally away from the enamel-dentine junction. In an interesting observation on the ultrastructural variations between individual teeth of *Kryptobaatar dashzevegi* located on the same mandible, these authors found that the molars appear to have a greater number of enamel tubules than the premolar. However, they cautioned that these supposed differences may be due to varying planes of sectioning.

Light versus electron microscopy

There are relatively few studies on the distribution and structure of enamel tubules in fossil reptiles and mammals. Most workers have mentioned their presence based on the observation of " hairlines " by optical microscopy, while SEM studies have recorded their presence relative to transversely and longitudinally sectioned (Fosse *et al.*, 1973 ; Sahni, 1979) or fractured (Lester & Archer, 1986) prisms and the inter-prismatic region (Carlson & Krause, 1982, 1985). It is possible that most of the so-called " hairlines " interpreted as tubule courses are in fact, either fractures between adjacent prisms accentuated by post-mortem processes or etch cracks developed between neighbouring prisms. The optical microscope does not have the required resolution to be effective in studying the structure, orientation or distribution of tubules in enamel of fossil reptiles and mammals. Scanning electron microscopy permits very adequate direct observation of tubules in both dentine and enamel and hence the reporting of the presence of tubules in samples by light microscopy may ultimately require revision through ultrastructural investigation.

The only primitive, fossil mammals studied extensively in this regard are the multituberculates (Fosse *et al.*, 1973, 1978; Sahni, 1979; Carlson & Krause, 1982, 1985). Together with site-associated marsupials, they clearly show that the possession of tubular enamel was a common characteristic of non-placental mammals in the Late Cretaceous (100 to 65 million years ago). Recent studies on the extant prototherian *Ornithorhynchus*, however, do not indicate the existence of characteristic prism-associated tubules (Lester & Boyde, 1986) although the fossil prototherian *Obdurodon insignis* does exhibit well-developed prismatic tubular enamel (Lester & Archer, 1986). In order to clarify the steps leading to the differentiation of non-therian and therian enamels, there is an urgent need for ultrastructural study of the Early Cretaceous (Albian) Trinity mammals of eutherian-metatherian grade from Texas, U.S.A.

Sampling and Quantification

An enormous problem in the characterization of species, both fossil and extant, with regard to a feature like enamel tubules is the element of variability resulting from the small areas sampled and the question of the known morphological origin of the samples with respect to the whole tooth. With fossils, there is the largely unknown natural history of the animal's earthly remains,

Source : MNHN, Paris

the question of possible damage versus normal functional change and the whole process of fossilization and subsequent preparation to take into account. Whole valuable specimens which may not be sectioned because of their significance to a museum collection present different kinds of fortuituous surfaces for examination by SEM. Different areas of enamel in the same specimen may show prisms and/or tubules to different degrees. There is a need for quantitative assessment in terms of predominence, extent, size, and location of tubules in order to make meaningful the term " tubular enamel ".

The building up of a catalogue of characters to overcome this inherent and induced variability is a massive task which really has only just begun (Fosse *et al.*, 1978, 1985; Carlson & Krause, 1985). The move away from morphological, qualitative assessment to stricter, quantitative morphometry is overdue and welcome. It is a question really of the future availability of time and resources as the level of interest is presently high and the physical methodologies for examination are available. It is to be hoped that somehow this logistical problem of massive data management and analysis can be tackled on a greater scale as the number of fossil finds, and the need for multi-disciplinary help with their interpretation, continue to increase.

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Source : MNHN, Paris

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Ultrastructural Study of Triconodont (Prototheria, Mammalia) Teeth from the Rhaeto-Liassic

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ABSTRACT

The enamel structure of the teeth of Triconodonta (Prototheria) has been the subject of several studies, with contradictory results. The authors conduct the same study, by the SEM, on Welsh material (Hettangian) and French material (Rhaetian). Their observations, which corroborate those of Osborn *et al.* (1979) demonstrate the existence, in this group, of a so-called preprismatic enamel, similar to that already described in Haramiyidae (Prototheria) and *Kuehneotherium* (Theria). Such an enamel is constituted of a juxtaposition of columns, formed by a diverging assemblage of hydroxyapatite crystals; these columns, grossly perpendicular to the enamel surface, are not separated by an interprismatic substance. It does seem that preprismatic enamel represents a structural stage linked with the complication of the dentition, a stage which may have been attained independently by several mammalian lineages. Dentine has also been examined, and various structures have been observed and described.

RÉSUMÉ

La structure de l'émail des dents de Triconodontes (Prototheria) a donné lieu à diverses études avec des résultats contradictoires. Les auteurs entreprennent à leur tour cette étude au SEM, sur du matériel du Pays de Galles (Hettangien) et de l'est de la France (Rhétien). Leurs observations, qui confirment celles d'Osborn *et al.* (1979), montrent l'existence dans ce groupe d'un émail dit préprismatique, comparable à celui déjà observé chez les Haramiyidés (Prototheria) et chez *Kuehneotherium* (Theria) ; c'est-à-dire que l'émail est constitué d'une juxtaposition de colonnes, elles-mêmes formées par un assemblage divergent de cristaux d'hydroxyapatite ; ces colonnes, grossièrement perpendiculaires à la surface de l'émail, ne sont pas séparées par un émail interprismatique. Il semble donc bien que l'émail préprismatique représente un stade structural lié à la complication de la denture, stade qui a pu être réalisé indépendamment dans différentes lignées de Mammifères. La dentine a également fait l'objet d'un examen et diverses structures y ont été observées et décrites.

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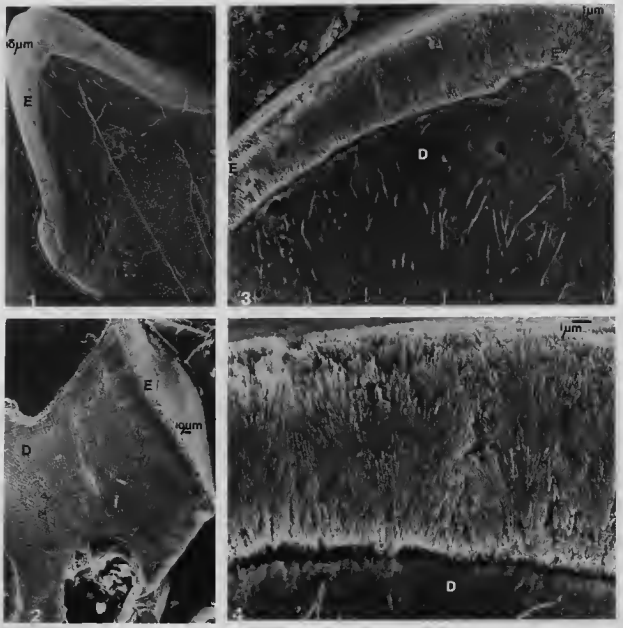

FIG. 1. — Bucco-lingual section of a triconodont molar (SNP 156W) from Saint-Nicolas-de-Port. A well differentiated layer of enamel (E) in the cuspal area becomes thinner along the cervical region. The presence of an artificial crack in enamel and dentine is indicated by an arrow. D = dentine.

FIG. 2. — Bucco-lingual section of another triconodont molar (SNP 479W) from Saint-Nicolas-de-Port with a thin layer of enamel (E). In the dentine (D) parallel circumferential lines (arrows) are visible around the pulp chamber.

FIG. 3. — A preprismatic pattern, characterized by the divergent orientation of the apatite crystals in each column, can be observed all along this enamel (E) of a triconodont molar (SNP 479W), in longitudinal bucco-lingual section: the presence of ramified dentinal tubules with calcified lumens is indicated by D.

FIG. 4. — Typical preprismatic pattern of the enamel columns of a triconodont molar (SNP 479W), with divergent orientation of the apatite crystals. Longitudinal bucco-lingual section. D = dentine.

Source : MNHN, Paris

Introduction

As early as the end of the Triassic (Rhaetian), three orders of mammals are known: the Theria Symmetrodonta (Kuehneotheriidae), the Prototheria Multituberculata (Haramiyidae) and the Prototheria Triconodonta (Morganucodontidae). The teeth of the two first families have been studied by us from the ultrastructural point of view (Frank *et al.*, 1984 ; Sigogneau-Russell *et al.*, 1985) and have been found to possess an enamel qualified as " preprismatic ": such an enamel consists of a juxtaposition of columns, each of which being constituted by hydroxyapatite crystals in a pinnate disposition, their c-axes forming a divergent angle with the main longitudinal axis of the columns; this angle is open towards the surface of the enamel. No interprismatic substance separates the columns.

As for the Triconodonta, their enamel has been the subject of several studies, whose results are somewhat contradictory: Moss & Kermack (1967) have described, in *Morganucodon*, a " pseudoprismatic " enamel, in which the axis of the crystallites varies gradually from an orientation perpendicular to the dentine-enamel limit to an inclination towards the cervical end of the crown. Osborn *et al.*(1979) have observed, in direct and polarized light, on longitudinal and transverse sections of the enamel of the teeth of *Eozostrodon* (probably from Wales), " close-packed hexagonal columns of crystals, each crystal deviating towards the center of its columns ". These columns are separated from each other neither by a sheath nor by an interprismatic substance. Such a description corresponds to what we have called preprismatic enamel. The authors note moreover the presence, in the enamel, of numerous tubules. Finally Grine *et al.* (1979), basing their observations on upper and lower molars of *Eozostrodon* (provenience not cited), testify to the existence, in this genus, of a true prismatic structure, with prisms of a circular or hexagonal section, separated by a well-differentiated interprismatic substance. These prisms even " show evidence of decussation between the dentine-enamel surface and the crown surface ".

Since we ourselves had at hand some triconodont material, we thought it would be interesting to undertake on these teeth the same study that we had previously conducted in *Kuehneotherium* and the Haramiyidae, in order to try to resolve this contradiction.

Material and Method

We used for this study two fragments of an upper molar of an undetermined triconodont from the Rhaetian of Saint-Nicolas-de-Port (France) (SNP 156W, SNP 479W) and a fragment of an upper molar of *Morganucodon (Eozostrodon)* from the Hettangian of Wales (Pontalun Quarry) (POQ 56) (numbers of the Musèum national d'Histoire naturelle, Paris).

The teeth were embedded in Epon 812. Using a grinding machine consisting of a rotating circular disk, a superficial bucco-lingual plane of section was prepared in the coronal part of the teeth. The prepared surface was polished with a fine diamond powder and slightly etched for 20-30 sec. with a 20 % citric acid solution. After coating with an Au-Pd layer in a Hummer Junior evaporator (Siemens, Karlsruhe), the prepared tooth surface was examined with a Jeol (Tokyo) JSM 35C scanning electron microscope (SEM) under 15KV. A new polished surface was then prepared by grinding off a further small portion of the tooth about 20 microns thick.

Following the same process of etching and coating, the new surface was studied by SEM. This procedure was pursued for half the thickness of the tooth. The other half was processed in the same way from one superficial side inwards in a plane perpendicular to the first sequence. This enabled the whole thickness of the tooth to be successively regarded and this in different planes: bucco-lingual, mesio-distal, transverse and oblique.

Results

A. *Ultrastructure of the two triconodont molars from Saint-Nicolas-de-Port*

These two teeth evince a well differentiated layer of enamel, which is wider in the cusp area and becomes progressively thinner along the

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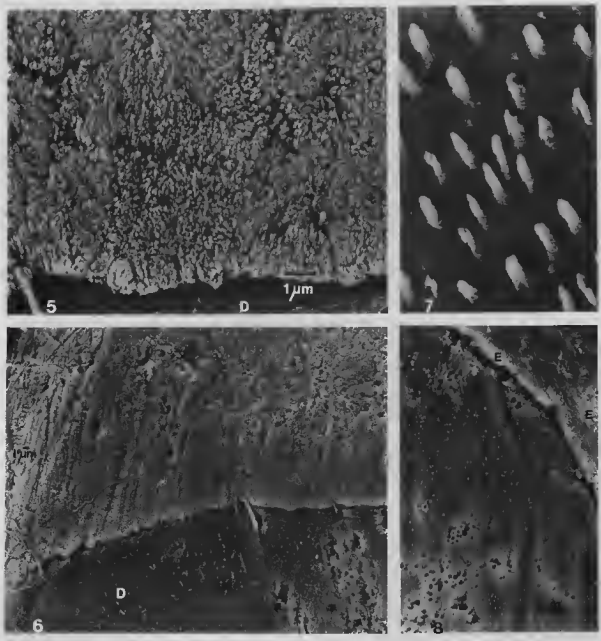

FIG. 5. — Transverse section across the enamel columns of a triconodont molar (SNP 479W). Most apatite crystals are cross-cut and show various domains with divergent orientation from the center of each column, producing a sort of sunbeam configuration. D = dentine.

FIG. 6. — Bucco-lingual section in a triconodont molar (SNP 479W). Ramified cracks filled by a calcified material are visible in the superficial dentine and enamel. In the dentine (D), irregular lesions of various size (to the right) are observed among dentinal tubules with calcified lumens.

FIG. 7. — Oblique section in dentinal tubules of a triconodont molar (SNP 156W). The lumens of these tubules are filled with a homogeneous calcified material.

FIG. 8. — Empty irregular lesions (lower left) are seen in peripheral dentine of a triconodont molar (SNP 479W) among dentinal tubules with white calcified lumens. E = enamel.

Source : MNHN, Paris

cervical region (Figs. 1 and 2). This enamel presents a typical preprismatic structure, that is to say, it is constituted here again of columns of crystals extending from the enamel-dentine junction to the enamel surface. Each column is itself formed of a diverging assemblage of fine hydroxyapatite crystals disposed as the barbs of a feather, in a pinnate disposition. The longitudinal axis of the column is grossly perpendicular to the enamel surface as well as to the enamel-dentine limit. The hydroxyapatite crystals are disposed on each side of the central axis with an angle open towards the enamel surface, an angle which varies from 30 to 40°. These results come from the examination of the longitudinal (Figs. 3, 4 and 9) as well as of the transverse (Fig. 5) sections. On the latter, the diverging character of the cristalline orientation inside each column is particularly distinct. The diameter of these columns varies from 4 to 5 microns. Finally, the columns are directly juxtaposed one next to the other, without the intermediary of an interprismatic substance and without the presence of a sheath. No tubules have been observed in this enamel.

The dentine, on the contrary, is rich in tubules extending from the pulp cavity towards the periphery, and all ending in the peripheral dentine close to the dentine-enamel junction (Figs. 3 and 4). The tubules often present ramifications and are devoid of peritubular dentine. The lumen of these tubules is obliterated by an amorphous calcified material which appears more dense than the intertubular dentine (Figs. 3, 7 and 9). This calcified material has the same aspect as the mineralized material filling cracks found in the enamel and dentine.

Indeed, the presence in these two layers of cracks or fissures has been observed; they were produced during fossilization and are filled with a dense and mineralized material (Figs. 6 and 9). Such cracks have their origin in the peripheral dentine and extend without discontinuity through the enamel, where they may branch in the deeper part and be found also at the surface of the enamel (Fig. 9). They can be distinguished from enamel tubules by the fact that they do not run parallel to the columns.

Thirdly, and due to the mode of preparation utilized, another kind of fissuration has been observed in enamel and dentine (Figs. 1, 8 and 10). These artefacts are empty and are in consequence easily distinguished from the preceding structures.

Finally, irregular galleries can be seen in places excavated into the peripheral dentine (Figs. 6, 8 and 10): these galleries, wider than the dentinal tubules, have a sinuous course and are linked with irregularly-shaped cavities dug also in the dentine. These cavities seem to correspond to *post mortem* saprophytic lesions such as those described by Sognnaes (1963).

The study of these triconodont molars at a low magnification revealed 3 to 4 coronal circumferential lines, running almost perpendicular to the axis of the dentinal tubules (2). These lines recall the apposition lines described in mammals during the development of dentine and are currently named contour lines of von Ebner.

B. *Ultrastructure of the Wales molar POQ 56*

The enamel covering this tooth is 15 to 20 microns thick. The same preprismatic structure can be observed, on longitudinal (Fig. 12) as well as on transverse (Figs. 11 and 13) sections. Each column, 4 to 5 microns wide, runs again from the enamel-dentine junction to the surface of the enamel. In each column, hydroxyapatite crystals diverge from the longitudinal axis at an angle of 15 to 20° and the angle thus opened between the diverging crystals of one column varies from 30 to 40°, this angle being open as in the preceding case, towards the surface of the enamel. These results are confirmed on oblique sections (Fig. 14). The absence of an interprismatic substance is also confirmed.

Cracks filled with a mineralized material and fissures due to the grinding-polishing process and devoid of calcified filling, are found here also in the enamel (Fig. 14). But no dentinal tubules have been observed.

Discussion

Concerning the dentine of our triconodont teeth, the absence of pericanalicular dentine is not surprising, since it does seem that this structure does not appear before the late Eocene (Remy, 1972).

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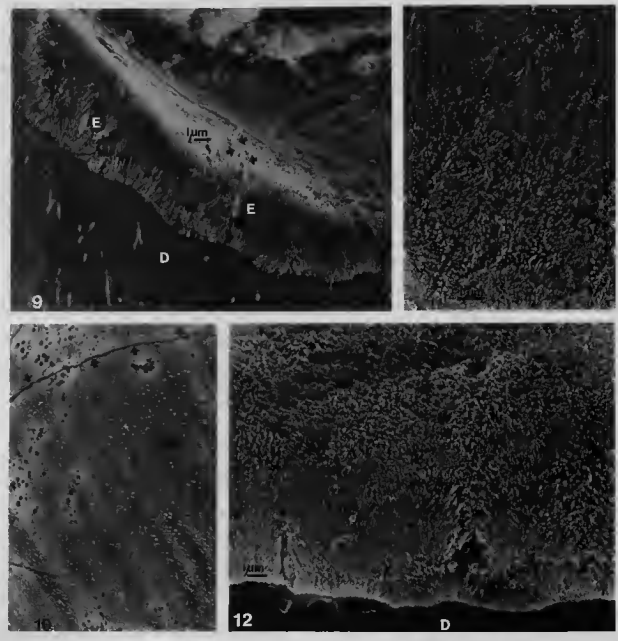

FIG. 9. — Simultaneous overview of the surface and a section of enamel (E) and dentine (D) of a triconodont molar (SNP 479W). The preprismatic pattern of the enamel is clearly visible. The presence, at the end of the enamel surface, of ramified cracks with homogeneous calcified content is indicated by arrows.

FIG. 10. — Transverse section in the dentine of a triconodont molar (SNP 479W). Note on the left side the presence of irregular hollow defects. The cross-sectioned dentinal tubules show calcified lumens (lower right). Note the presence of an empty crack in the upper part (arrows).

FIG. 11. — Transverse section of preprismatic enamel of a molar (POQ 56) from Wales. Note the presence of apatite crystals with a divergent " sunbeam " configuration.

FIG. 12. — Preprismatic pattern with repetitive divergent orientation of the apatite crystals in a longitudinal buccо-lingual section of enamel from a molar (POQ 56) from Wales.

Source : MNHN, Paris

As for the dentinal tubules, their abundance here conforms to what is known in reptiles and mammals. Besides, Grine *et al.* acknowledge that their absence, in their observations of *Eozostrodon*, may be no more than an artefact.

In the enamel, the absence of tubules, which contradicts the observations of Osborn *et al.*, is consistent with what we have found in the teeth of Haramiyidae and of *Kuehneotherium*. And it is to be remarked that, in two Prototheria (one

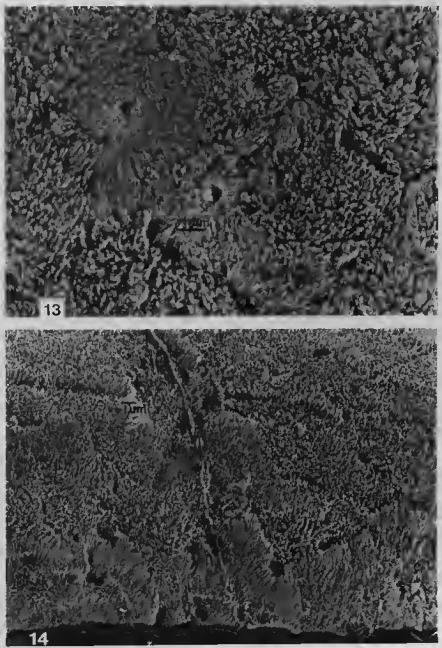

FIG. 13. — Higher magnification of a transverse section in preprismatic enamel of a molar (POQ 56) from Wales. The "sunbeam" divergent configuration of the apatite crystals of each column is clearly visible.

FIG. 14. — Oblique section in preprismatic enamel of a molar (POQ 56) from Wales. Note the presence of a vertical crack with calcified contents (arrows) in the center of this micrograph.

Source : MNHN, Paris

docodont, one multituberculate) from the late Jurassic, Fosse *et al.* in 1985, found these tubules to be " very scarce ".

As regards the nature of the enamel, the preprismatic structure differs from the "pseudo-prismatic " enamel described by Moss & Kermack (1967). Our findings do not corroborate either the observations made by Grine *et al.*, all the less so that the columns illustrated by these authors have a smaller diameter (3 μm) and that they are decussating, while our columns are running straight from the dentine-enamel junction to the surface of the enamel. This preprismatic structure is on the contrary consistent with that described by Osborn *et al.* in *Eozostrodon* and, as remarked by these authors, constitutes a perfect transition between the aprismatic enamel of reptiles and the truly prismatic enamel of later mammals.

Besides, the same preprismatic structure has been found, not only by us in the Haramiyidae and in *Kuehneotherium* (where the columns are about 6 μm wide), but also by Fosse *et al.* in the two forms from the late Jurassic, with " prisms " of dimensions similar to those of our triconodonts (5 μm). Thus the preprismatic structure would really represent a structural stage connected with the morphological complication of the dentition and also perhaps (Grine *et al.*) with their unique replacement; and these preprisms are considered as homologous to the columns of later mammals.

To conclude, the enamel ultrastructure appears to be uniform in the early mammals. But it does seem that the truly prismatic structure (with interprismatic substance) has appeared twice in the evolution of mammals: in Multituberculata and in Theria. It may thus have been the case also for the preprismatic structure, and the uniformity noted in the Triassic forms does not constitute an argument in favor of the monophyletism of mammals.

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Source : MNHN, Paris

Évolution de la Structure de l'Émail chez les Proboscidea Primitifs : Aspects Phylogénétique et Fonctionnel

P. BERTRAND

ABSTRACT

The ensemble of the groups of primitive Proboscidea: Barytheriidae, Deinotheriidae, Moeritheriidae, Gomphotheriidae, Phiomiidae, and some genera of Sirenians, Desmostylians and Anthracobunidae have been investigated through a comparative study of the dental enamel structure. The analysis of the structure is based upon various methodological approaches: scanning electron microscope (SEM), thin slides, micrographs, tandem scanning reflected light microscope and a tridimensional explanation of the enamel organization. The study of enamel structures has been carried out both at the prismatic level (prisms pattern, distribution or relative size) and at the Hunter-Schreger bands level, the organization of which (distribution, width, pattern of decussation) exhibits in some groups remarkable functional and systematic characteristics.

Three fundamental patterns of enamel organization coexist within primitive Proboscidea:

— Moeritheriidae have a simple structure, nearly comparable to that of primates: Hunter-Schreger bands are regular and the pattern of decussation is only horizontal.

— Barytheriidae and Deinotheriidae possess a very particular organization, with Hunter-Schreger bands stretching through the whole enamel thickness, and a high complexity of the decussation pattern as an important vertical component comes out clearly. The two combined patterns induce an irregular zonation, with Hunter-Schreger bands running alter-

RÉSUMÉ

L'ensemble des groupes de Proboscidea primitifs : Barytheriidae, Deinotheriidae, Moeritheriidae, Gomphotheriidae, Phiomiidae, ainsi que certains genres de Siréniens, de Desmostyliens, et d'Anthracobunidae a fait l'objet d'une étude comparative de la structure de l'émail dentaire. L'analyse de la structure est basée sur une approche méthodologique variée : microscope électronique à balayage (MEB), lames minces, macrophotographies, tandem scanning reflected light microscope, et une interprétation tridimensionnelle de l'organisation de l'émail. L'étude de la structure de l'émail a été réalisée tant au niveau prismatique (type d'émail, répartition, importance relative), qu'au niveau des bandes de Hunter-Schreger dont le plan d'organisation (répartition, largeur des zones, mode de décussation) présente dans certains groupes des caractéristiques fonctionnelles et systématiques remarquables.

Trois types fondamentaux d'organisation coexistent chez les Proboscidea primitifs :

— Les Moeritheriidae avec une structure simple, comparable à celle d'un primate ; les bandes de Hunter-Schreger sont régulières, et la décussation est uniquement horizontale.

— Les Barytheriidae et Deinotheriidae possèdent une organisation très particulière, avec des bandes de Hunter-Schreger s'étendant sur la totalité de l'épaisseur, et une complication du mode de décussation : il apparaît une composante verticale importante. Les deux modes de décussation combinés

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D.E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 109-124.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

nately upward (occlusally) and downward (cervically).

— Gomphotheriidae have developed a considerable thickness of parallel prisms in the external portion of the enamel, although horizontal decussation still occurs at the enamel-dentine junction (EDJ) level.

The existence of phylogenetic relationships between the Barytheriidae and the Deinotheriidae is suggested from the structural organization of the enamel. Differences of enamel spatial organization are probably linked with differences in masticatory requirement: lophodonty or bunodonty.

provoquent l'apparition d'une zonation irrégulière, à bandes de Hunter-Schreger orientées alternativement en direction occlusale ou cervicale.

— Les Gomphotheriidae ont développé une épaisseur considérable d'émail à prismes parallèles entre eux dans la zone périphérique externe bien qu'une zone à décussation horizontale persiste au niveau de la limite émail-dentine (EDJ).

L'existence de relations phylogénétiques entre Barytheriidae et Deinotheriidae est proposée sur la base de l'organisation structurale de l'émail. Les différences d'organisation tridimensionnelle de l'émail sont probablement liées aux différences de mode masticatoire : lophodontie ou bunodontie.

Introduction

L'étude de l'évolution de la structure de l'émail mammalien a connu, ces dernières années (Kozawa, 1984 ; von Koenigswald, 1985), un essor considérable, principalement lié au développement de la microscopie à balayage (Boyde, 1964, 1969). Néanmoins, de nombreuses interrogations persistent quant aux utilisations potentielles de la microstructure dentaire dans la construction d'hypothèses phylogénétiques, ou dans la confrontation des phylogénies aux données microstructurales. Les récents travaux de von Koenigswald (1980), ou de Martin (1985) semblent indiquer que l'on peut étudier l'évolution de l'émail jusqu'au niveau spécifique. Cependant les effets du parallélisme entre groupes, ou de la divergence structurale intergroupe sont encore mal appréhendés, aussi importe-t-il d'étudier des lignées phylétiques connues, et suffisamment longues pour observer l'évolution des structures.

En outre, les travaux les plus récents (Stern *et al.*, 1985) montrent la nécessité d'évaluer préliminairement la nature des variations intra-dentaires, individuelles et spécifiques, ainsi que d'adopter un protocole expérimental adéquat.

Ces études ont été jusqu'ici principalement axées sur les primates (Boyde *et al.*, 1982 ; Martin, 1985), les rongeurs (von Koenigswald, 1980), les multituberculés (Carlson *et al.*, 1985), voire certains mammifères primitifs (Moss, 1969 ; Frank *et al.*, 1984). Néanmoins, un groupe tel que les téthythères n'a fait l'objet que de rares études (Ijiri *et al.*, 1948 ; Boyde, 1964 ; Kaibara, 1968 ; Kozawa, 1978).

La présente étude, qui porte essentiellement sur les Proboscidea primitifs, n'est qu'une partie d'un travail ayant pour but d'évaluer la variation structurale ainsi que l'évolution de l'émail dentaire chez les Proboscidea et les groupes apparentés, par comparaison avec la phylogénie connue et la différenciation morphologique des dents.

Les Proboscidea de l'Éocène-Oligocène constituent la base de cette étude, car ils forment un ensemble phylogénétique hétérogène, possèdent des modes masticatoires très différents et n'ont, jusqu'ici, jamais fait l'objet d'études comparatives de la structure de l'émail dentaire.

Méthodologie

Les dents étudiées proviennent des groupes suivants (Fig. 1) : Barytheriidae : *Barytherium grave* (Éocène, Lybie), *Numidotherium koholense* (Éocène, Algérie) ; Deinotheriidae : *Prodeinotherium bavaricum* (Miocène, France), *Deinotherium bozasi* (Pliocène, Kenya) ; Gomphotheriidae : *Gomphotherium angustidens* (Miocène, France) ; Moeritheriidae : *Moeritherium lyonsi* (Éocène, Algérie) ; les genres *Phiomia* et *Paleomastodon* (Oligocène, Égypte), ainsi que des Sirenidae, Desmostylidae et Anthracobunidae (*Jozaria palustris, Lammidhania wardi* : Éocène, Pakistan).

Dans tous les cas, la détermination taxonomique des spécimens est connue, d'après les observations morphologiques, jusqu'au niveau spécifique, ainsi que la position des dents et fragments sur la rangée dentaire.

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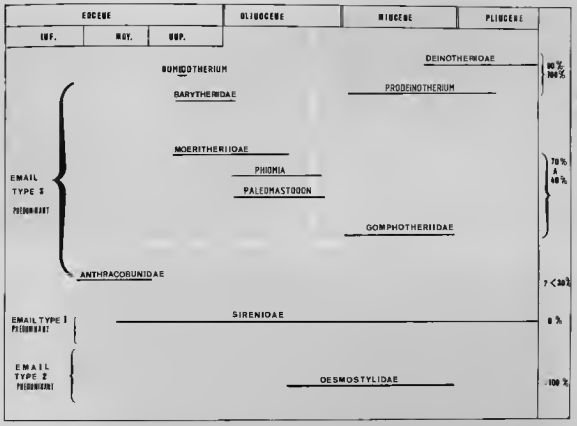

FIG. 1. — Position stratigraphique des différents groupes de Proboscidea primitifs. Les formes sont réunies suivant le type prédominant d'émail (selon Boyde, 1964 and Sazaki, 1983). Le taux de décussation (voir texte) sur une coupe longitudinale dans une face mésiale de molaire est figuré afin de monirer les différences entre groupes (le chiffre mentionné pour les Anthracobunidae correspond à *Lammidhania wardi* et *Jozaria palustris*).

Diverses méthodes ont été employées afin d'appréhender la diversité structurale :

— Microscopie électronique á balayage (Boyde, 1984a) : les échantillons sont d'abord polis, puis soumis á une légère attaque acide (mordançage) et enfin métallisés et examinés á divers grossissements (entre × 30 et × 1 800), suivant les structures, prismes ou bandes de Hunter-Schreger, à mettre en évidence.

— Lames minces et microscopie polarisante.

— Macrophotographie en lumiére incidente : les macrophotographies permettent, à partir de préparations métallisées, de mettre en évidence les bandes de Hunter-Schreger et leur répartition dans la totalité d'un plan de coupe. Cette technique acquiert un intérêt particulier pour les observations globales (grossissement compris entre × 1 et × 30) et pour les spécimens dont les dimensions sont incompatibles avec une observation en microscopie électronique. L'interprétation des zones est aisée, car la réflexion de la lumiére par les prismes est différente suivant leur plan de coupe (Fig. 2B), ainsi que l'avaient déjà noté Rensberger et von Koenigswald (1980).

— Tandem scanning reflected light microscope (TSRLM) : nous devons à la cordialité du Professeur A. Boyde d'avoir pu réaliser de nombreuses photographies à l'aide du tandem scanning reflected light microscope (Boyde *et al.*, 1983, 1984) qui permet des observations tangentielles de l'émail sans aucune préparation préalable.

L'ensemble des formes étudiées a été observé á l'aide d'au moins trois des précédentes méthodes et sur un échantillonnage de plusieurs dents d'individus différents (molaires et prémolaires).

Les résultats présentés dans ce travail portent essentiellement sur la structure des molaires et

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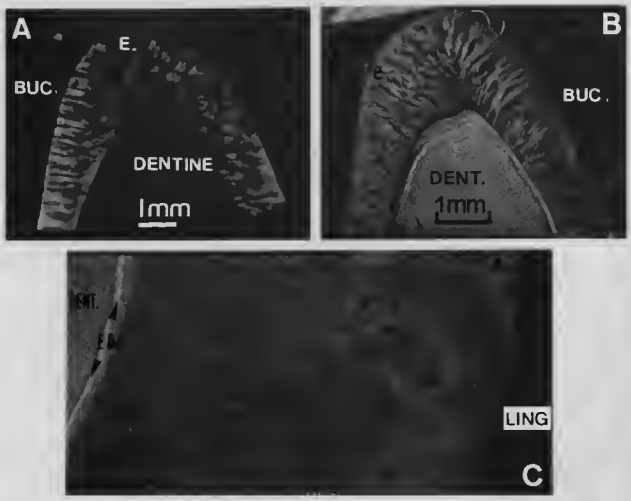


FIG. 2. — *Numidotherium koholense*, Incisive en coupe longitudinale. La même dent a été utilisée pour les trois préparations. Comparaison des résultats obtenus par diverses méthodes. Les macrophotographies, quelle que soit la position de la source lumineuse, font toujours apparaître les diazones (zones dans lesquelles les prismes sont coupés perpendiculairement à l'axe c des crystallites) en sombre : absorption partielle ou totale de la lumière, et les parazones (zones à prismes coupés longitudinalement) ; en clair : réflexion partielle ou totale de la lumière. Les résultats des différentes méthodes sont tout à fait comparables quant à l'interprétation tridimensionnelle de la structure de l'émail. (Buc. = face buccale ; Dent. = dentine ; E. = émail ; Ling. = face linguale).

A, Lame mince (épaisseur < 50 μ). Microscopie polarisante. Les bandes de Hunter-Schreger sont nettement visibles, ainsi que leur disposition.

B, Macrophotographie en lumière incidente. Les bandes de Hunter-Schreger visibles grâce à cette méthode sont strictement comparables à celles observées en microscopie polarisante, ou en microscopie électronique à balayage.

C, Microscopie électronique à balayage (MEB) : polissage au diamant (0,25 μ), mordançage avec H_3PO_4 (3 %, 50 secondes), métallisation à l'or et observation à 10 Kv.
(EDJ. = jonction émail-dentine ; dia. = diazone ; par. = parazone).

prémolaires, afin d'autoriser une comparaison entre dents homologues suivant les différents groupes.

Les caractères utilisés pour l'étude de la structure de l'émail doivent être soigneusement choisis : taille, type de prismes (Boyde, 1964), mode d'empilement, mais surtout variations de la répartition des bandes de Hunter-Schreger sur toute l'épaisseur et suivant différents plans, ainsi que l'inclinaison et le trajet des prismes par rapport à l'interface dentine-émail.

L'estimation de la variation individuelle, intra-

Source : MNHN, Paris

dentaire et entre individus de la même espèce, a été établie au préalable sur l'espèce *Numidotherium koholense* Mahboubi *et al.*, 1986. Les premiers résultats « Structural variations in the enamel of the Proboscidean: *Numidotherium koholense* » (P. Bertrand, en préparation), montrent la répétitivité des observations au niveau spécifique. Les variations intradentaires sont souvent plus importantes que les variations individuelles, mais négligeables par rapport aux différences interspécifiques.

Par ailleurs l'analyse tridimensionnelle de la structure des dents a été réalisée dans la majorité des cas, par l'observation de tous les plans suivants : coupes tangentielles á plusieurs niveaux et différents sites, coupes bucco-linguales (i.e. : transversales), mésio-distales (i.e. : longitudinales), ou perpendiculaires à l'axe vertical de la dent (i.e. : horizontales).

Le mode de décussation trés particulier de l'émail des Proboscidea (irrégulier), fournit á cet égard un matériel exceptionnel pour comprendre l'évolution de l'émail au sein d'une lignée mammalienne.

Résultats

L'étude peut s'effectuer soit au niveau de la structure et de l'origine des unités prismatiques telles qu'elles ont été définies par Shobuzawa (1952), Boyde (1964) et Sasaki (1983), soit sur l'organisation spatiale de ces unités.

A. *Niveau prismatique*

Toutes les espèces étudiées présentent un ou plusieurs des 3 types fondamentaux d'organisation des crystallites, au niveau des prismes. Néanmoins, la répartition dans la dent de ces types de prismes dépend de la position de l'observation dans l'épaisseur de l'émail ainsi que du groupe auquel appartient le spécimen.

Les Desmostyliens, trés souvent rapprochés des Proboscidea, s'en distinguent aisément par un émail de type 2 (Fig. 3B) : prismes alignés en rangées, séparées par des parois d'émail interprismatique (Shobuzawa, 1952 ; Boyde, 1964 ; Sasaki *et al.*, 1983). Cependant le type 1 se rencontre dans les quelques microns qui jouxtent la limite avec la dentine, ainsi qu'à la périphérie de l'émail.

Tous les autres groupes présentent, lorsque les dents (molaires et prémolaires) ne sont pas usées, la zonation suivante :

a. — Émail de type 1 (Fig. 3D) : quelques microns au niveau de la limite émail-dentine (EDJ) ; l'épaisseur est variable suivant les groupes.

b. — Émail de type 3 dans l'épaisseur de l'émail (sans passage observable au type 2) ; cette zone est généralement subdivisée en une zone interne, où les prismes peuvent décusser et une zone externe à prismes parallèles entre eux. Les épaisseurs respectives de ces deux zones sont très variables et liées au mode de décussation des prismes. C'est au niveau de l'émail de type 3 (Figs. 3E, F), que peuvent se reconnaître des différences morphologiques spécifiques.

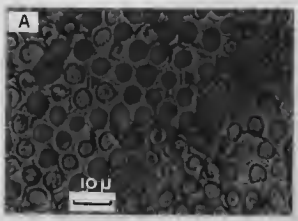
c. — Une zone périphérique externe de type 1 (Fig. 3C) et d'épaisseur variable (souvent inférieure á 20 microns).

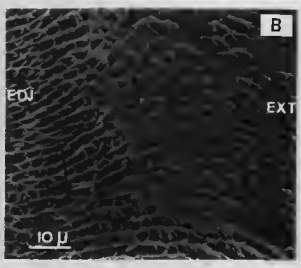
Chez les Siréniens l'émail de type 1 (c'est-à-dire á prismes ronds, entourés d'un émail interprismatique épais), occupe une zone externe représentant approximativement 50 % de l'épaisseur (Fig. 3A), quels que soient la position sur la dent, ou le groupe considéré : *Dugong* (actuel, Australie) ; *Trichechus* (actuel, Floride) ; *Metaxytherium* (Miocéne supérieur, Algérie). Cependant, contrairement aux observations antérieures (Boyde, 1965 ; Kozawa, 1984 ; Sahni, 1981b), nous considérons que la zone interne (Fig. 4A) est composée d'émail de type 3.

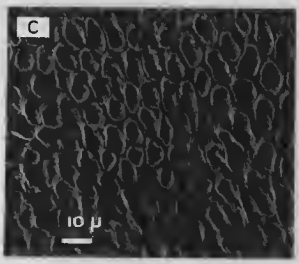
Dans toutes les formes, il est observé une augmentation du diamétre des prismes depuis la limite émail-dentine jusqu'à la surface externe. Cette augmentation est plus marquée dans la zone occlusale que cervicale, et plus importante dans les formes non-lophodontes.

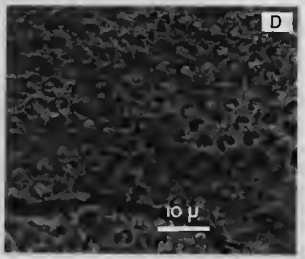
La forme des prismes peut de même être utilisée pour caractériser certaines espéces, mais il existe une forte variation intra-dentaire qui impose de réaliser l'étude préalable de plusieurs spécimens. Néanmoins la forme des prismes de *Gomphotherium angustidens* (Fig. 3F), trés allongée au niveau de la tête du prisme, se distingue aisément de celle d'un barythére (Fig. 3E) ou d'un deinothére.

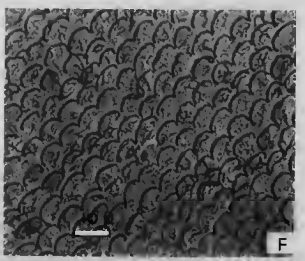
Source : MNHN, Paris











Source : MNHN, Paris

De fait, il est extrêmement important de connaître les position et profondeur exactes d'un échantillonnage tangentiel.

B. *Décussation et bandes de Hunter-Schreger*

Les bandes de Hunter-Schreger sont des phénoménes optiques observables en microscopie polarisante, qui correspondent à l'interception par le plan d'observation de groupes de prismes coupés alternativement longitudinalement et transversalement. En microscopie á balayage il s'agit respectivement des parazones et des diazones qui représentent en deux dimensions un phénomène tridimensionnel : la décussation, qui décrit le déplacement relatif de la trajectoire des prismes par rapport à l'axe vertical de la dent (Boyde, 1969).

Cette trajectoire des prismes n'étant ni rectiligne ni perpendiculaire à l'interface émail-dentine, on peut observer deux types de déplacements : horizontaux (buccal-lingual ou mésial-distal) et verticaux (occlusal-cervical) ; ces deux types peuvent éventuellement être combinés.

L'organisation et la répartition des bandes de Hunter-Schreger sont les caractéristiques les plus intéressantes de la structure de l'émail.

Le type 1 (Boyde, 1964 ; Sasaki *et al.*, 1983) est toujours associé, chez les mammifères, á des prismes sans décussation et tous parallèles entre eux (Fig. 4A : zone externe). Cette organisation homogène des prismes est aussi associée, dans tous les autres groupes, á l'émail de type 1 périphérique.

Contrairement aux autres formes dont l'émail est aussi principalement composé d'émail de type 3 (carnivores, primates), les Proboscidea présentent une organisation des bandes de Hunter-Schreger très irrégulière. Ce modèle n'apparaît néanmoins que progressivement au cours de l'évolution de la famille.

Inclinaison et orientation des zones par rapport á la limite émail-dentine (EDJ), proportion des zones décussantes, nombre et taille des zones, peuvent être utilisés pour définir les caractéristiques de l'émail et éventuellement pour regrouper les différentes espèces au niveau taxonomique.

Ainsi, le pourcentage de décussation présente une variation notable suivant les groupes (Fig. 1). On peut estimer suivant un plan de référence (longitudinal, horizontal, transversal ou tangentiel) l'extension des bandes de Hunter-Schreger par rapport á l'épaisseur totale de l'émail. Cette mesure est répétée de dix á vingt fois á différentes positions au niveau de la mi-couronne, ce qui permet d'obtenir un pourcentage moyen de décussation sur un plan donné. (Fig. 1 : coupe longitudinale).

Moeritheriidae

Les bandes de Hunter-Schreger ont une répartition qui suit les grands traits de la morphologie dentaire, mais une coupe typique dans une molaire (Fig. 4B) est trés proche de la structure observable chez un homme (Skobe *et al.*, 1980 ; Stern *et al.*, 1985) : une zone interne á bandes de Hunter-Schreger régulières, qui occupent environ

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Fig. 3.

A, *Metaxytherium sp.* Spécimen non numéroté. MEB. Molaire (M_1). Coupe tangentielle au niveau de la zone externe d'une face labiale, approximativement 500 µ sous la surface externe. ip = émail interprismatique ; p = prisme.

B, *Desmostylus hesperus.* Miocéne, Montana. Spécimen non numéroté. MEB. Molaire inférieure, coupe horizontale á mi-couronne. Détail de la structure de l'émail de type 2 (niveau EDJ). On observe une décussation des prismes. ↗ souligne les différences d'orientation des prismes. EDJ. = vers limite émail-dentine ; EXT. = vers surface externe.

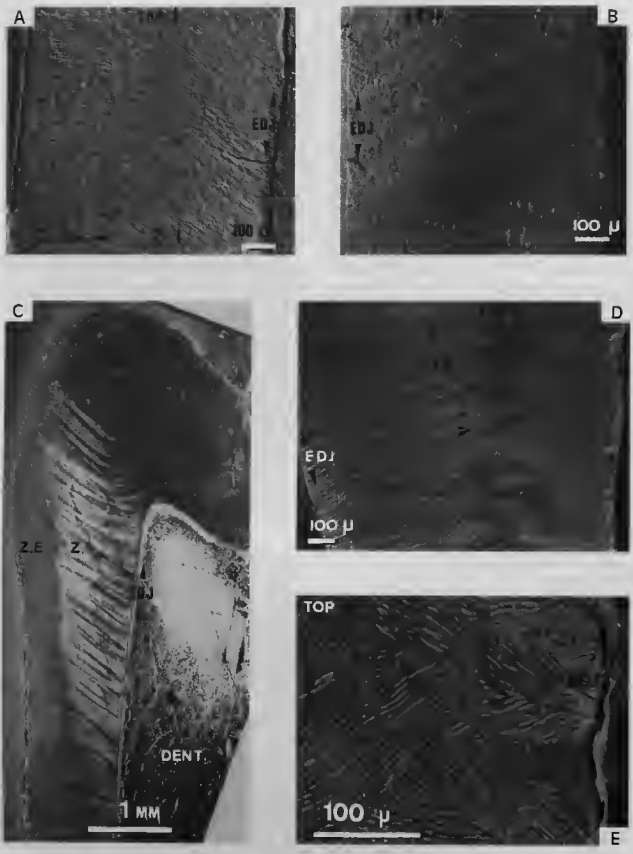
C, *Deinotherium bozasi.* Spécimen non numéroté. MEB. Molaire supérieure : coupe tangentielle, face buccale, au niveau de la surface externe pour montrer l'émail de type 1 périphérique.

D, *Numidotherium koholense.* Spécimen non numéroté. Prémolaire inférieure (P_3). MEB. Cassure approximativement longitudinale. Exemple d'émail de type 1 au niveau EDJ : la dentine a été détachée afin de montrer la limite EDJ depuis l'intérieur de la dent.

E, *Numidotherium koholense.* Spécimen non numéroté. MEB. Coupe longitudinale dans une prémolaire inférieure (P_4). Détail de l'organisation des prismes coupés perpendiculairement á l'axe principal. On comparera cette structure avec celle de la photographie F. (DIA = diazone ; PAR = parazone).

F, *Gomphotherium angustidens.* Molaire n° SEP 224. MEB. Coupe tangentielle dans l'émail au niveau de la zone externe á prismes parallèles. Émail á prismes de type 3. Noter l'organisation des prismes en rangées.

Source : MNHN, Paris



Source : MNHN, Paris

65 % de l'épaisseur, et une zone externe composée de prismes parallèles entre eux (émail de type 3).

La largeur des parazones est importante (80 µ) au niveau cervical, puis diminue progressivement jusqu'au niveau des cuspides. Les prismes suivent une trajectoire rectiligne depuis la limite EDJ jusqu'à la surface externe dans la région cervicale, alors qu'au niveau des conules, leur trajectoire est sinueuse et incurvée vers le sommet (Fig. 4C) ; situation qui est comparable à celle de l'homme (Hirota, 1982), ou d'un Suidae. La décussation s'effectue uniquement horizontalement et aucune zone inclinée cervicalement n'est observée.

Il n'existe qu'une faible différenciation intradentaire : inclinaison des prismes par rapport à EDJ, zones plus rectilignes sur la face mésiale d'un conule que sur la face distale, et les variations reflètent généralement le polymorphisme dentaire : prémolaires non molarisées, molaires.

Barytheriidae

L'émail (type 3) de ces formes : *Barytherium grave, Numidotherium kolohense* est quasiment identique et présente un mode de décussation tout à fait remarquable au sein des mammifères : le plan d'organisation des molaires et prémolaires en zone interne décussante et zone externe à prismes parallèles disparaît pour être remplacé par une décussation s'étendant sur la quasi-totalité de l'épaisseur, qui se caractérise par des bandes de Hunter-Schreger sinueuses, souvent anastomosées et de largeur variable depuis la limite EDJ jusqu'à la surface externe (Fig. 4D). Les bandes de Hunter-Schreger sont globalement orientées vers la surface occlusale, et il existe une couche externe d'émail de type 1.

Les variations entre les zones occlusale et cervicale sont par contre négligeables et il y a perte de l'aspect concentrique des bandes de Hunter-Schreger autour du sommet des cuspides.

Par ailleurs, il existe une différenciation (spécialisation ?) intradentaire car les molaires inférieures (faces mésiale et distale), les prémolaires inférieures (face mésiale), ainsi que les molaires supérieures (face distale) présentent toujours un aspect typique (Fig. 4E). La décussation n'est plus seulement horizontale, mais aussi verticale : les nappes de prismes sont moins sinueuses, et souvent orientées alternativement cervicalement et occlusalement. Cette structure induit l'aspect particulier de l'émail en macrophotographie (Fig. 5B). Ces faces, même non usées, ne présentent jamais d'émail de type 1 à la périphérie et le pourcentage de décussation est supérieur à 95 % (Fig. 5C). Les stries de Retzius sont particulièrement visibles sur les faces latérales des dents, ainsi que les périkymatas (Fig. 4D).

Deinotheriidae

Les deux formes étudiées *Prodeinotherium* et *Deinotherium* ont une structure très semblable, malgré la différence d'épaisseur de l'émail. Les bandes de Hunter-Schreger sont quasi-rectilignes,

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Fig. 4.

A, *Trichechus manatus*. Spécimen non numéroté. Molaire inférieure. MEB. Coupe longitudinale dans une face mésiale du premier lophe. Organisation de l'émail en deux zones avec des prismes tous parallèles et absence de décussation : une zone externe (Z.E.) à prismes perpendiculaires à la surface externe (émail de type 1), et une zone interne (Z.I.) à prismes orientés occlusalement (émail de type 3). EDJ. = limite émail-dentine.

B, *Moeritherium lyonsi*. Spécimen non numéroté. Molaire inférieure (M_2). Coupe longitudinale, face mésiale à mi-couronne. MEB. Le spécimen n'est pas poli, et a subi une attaque acide très légère. Noter l'extension et la régularité des bandes de Hunter-Schreger (parazones-diazones).

C, *Moeritherium lyonsi*. Spécimen non numéroté. Prémolaire inférieure (P_3). Macrophotographie en lumière incidente. Coupe transversale, face labiale. On remarque l'arrangement concentrique des bandes de Hunter-Schreger au niveau du sommet de la cuspide. DENT. = dentine ; Z.I. = zone interne à décussation des prismes, Z.E. = zone externe sans décussation.

D, *Numidotherium koholense*. Spécimen non numéroté. MEB. Coupe transversale dans une molaire supérieure, face linguale à mi-couronne. On notera l'extension de la décussation sur la quasi-totalité de l'épaisseur de l'émail ainsi que le trajet sinueux des bandes de Hunter-Schreger. Les stries de croissance (= Str.) sont particulièrement visibles.

E, *Numidotherium koholense*. Spécimen non numéroté. MEB. Coupe transversale dans une prémolaire (P_3) inférieure, face labiale à mi-couronne. Détail de l'organisation de l'émail au niveau EDJ. La décussation présente une composante verticale bien visible sur cette photographie, et une composante horizontale. Ceci donne un aspect irrégulier à la décussation car aucune composante n'est privilégiée.

Source : MNHN, Paris

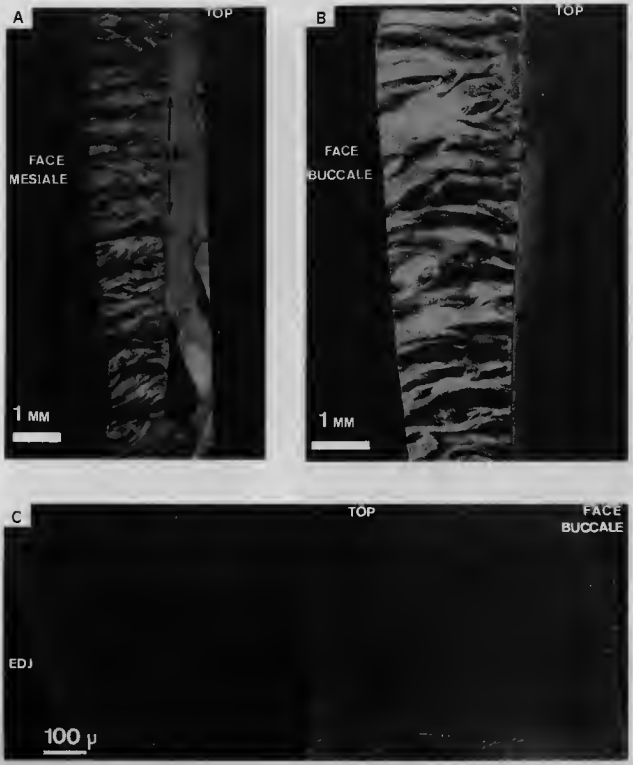


FIG. 5

A, *Prodeinotherium bavaricum*. Spécimen non numéroté, coll. Lab. Pal. Vert. Pal. Hum. Macrophotographie en lumière incidente. Molaire inférieure. Coupe longitudinale, face mésiale. La décussation est dans ce cas verticale et horizontale, ce qui provoque l'aspect alternatif des bandes de Hunter-Schreger. (TOP = sommet du lophe).

B, *Barytherium grave*. Spécimen non numéroté. Macrophotographie en lumière incidente. Prémolaire inférieure (P_4). Coupe transversale, face buccale. Noter l'organisation très complexe des bandes de Hunter-Schreger. On comparera cette structure avec celle des Moeritheriidae (Fig. 4C).

C, *Numidotherium koholense*. Spécimen non numéroté. MEB. Molaire supérieure (M_3), face buccale. Coupe transversale à mi-couronne. Détail de l'organisation des bandes de Hunter-Schreger avec décussation irrégulière.

Source : MNHN, Paris

anastomosées, et s'étendent sur la totalité de l'épaisseur : le pourcentage de décussation est voisin de 100 % (Fig. 5A). La largeur des zones est très variable mais ne présente pas de gradient cervico-occlusal.

Dans l'émail des molaires inférieures (faces distales et mésiales) et supérieures (faces distales), les bandes de Hunter-Schreger alternent très visiblement et sans intermédiaire en direction cervicale et occlusale, sur une très importante zone interne, alors que la zone externe présente des prismes plus rectilignes et dirigés perpendiculairement à la surface externe. Il n'apparaît pas d'émail de type 1 visible sur ces faces.

Il existe une différenciation intra-dentaire, car les faces latérales des lophes possèdent des zones plus sinueuses, orientées nettement vers la surface occlusale, ainsi qu'une couche externe de type 1.

Deux modes de déplacement des prismes sont donc combinés : déplacement vertical et déplacement latéral particulièrement visible en coupe horizontale. Ce mode de décussation est observable dès la surface externe en vue tangentielle. Cette structure typique est identique dans les molaires et les dents déciduées.

Gomphotheriidae

(Gomphotherium angustidens, Gomphotherium sp.*)*

La structuration de l'émail est très différente de celle des groupes précédents, puisque la présence de bandes de Hunter-Schreger est restreinte á une courte zone prés de la limite émail-dentine : les prismes dans cette zone sont sinueux, et créent des bandes de Hunter-Schreger de largeur variable (la largeur diminue progressivement à partir de la limite EDJ vers l'extérieur), dans les plans horizontaux et parfois verticaux (Fig. 6A). Cette zone décussante ne représente que 40 á 45 % de l'épaisseur totale. Le reste de l'épaisseur est constitué de prismes de type 3, tous arrangés parallélement entre eux (Fig. 3E) et inclinés vers le sommet des conules avec un angle moyen de 60°.

Il n'existe pas de différenciation intra-dentaire : les faces linguale, buccale et mésiale sont quasiment identiques, ni de variations significatives entre dents différentes.

Phiomia et *Paleomastodon*

Le genre *Phiomia* n'a pu être étudié qu'á l'aide du microscope TSRLM (Boyde *et al.*, 1983, 1984), et de moulages sur fracture. Cependant les observations réalisées permettent de décrire, dans une molaire, la zonation suivante :

— Émail de type 1 : près de la surface externe (environ 20 μ).

— Émail de type 3 : zone externe á prismes parallèles, puis zone interne décussante représentant approximativement 40 à 50 % de l'épaisseur.

D'autre part, nous avons pu étudier l'espéce *Paleomastodon beadnelli*, dont les molaires présentent depuis la limite EDJ jusqu'á la surface externe les caractéristiques suivantes (Fig. 6B) :

— Émail de type 1 : quelques microns au niveau EDJ.

— Émail de type 3 : — á décussation horizontale, s'étendant sur presque 70 % de l'épaisseur totale. La décussation au niveau EDJ est néanmoins régulière et aucune zone dirigée cervicalement n'est observée : les prismes sont tous orientés en direction occlusale.

— à prismes parallèles entre eux, et nettement orientés perpendiculairement á la surface externe, dans une zone périphérique par rapport á la précédente.

— Émail de type 1 sur une faible épaisseur ($< 15\ \mu$) au niveau de la surface externe de la dent.

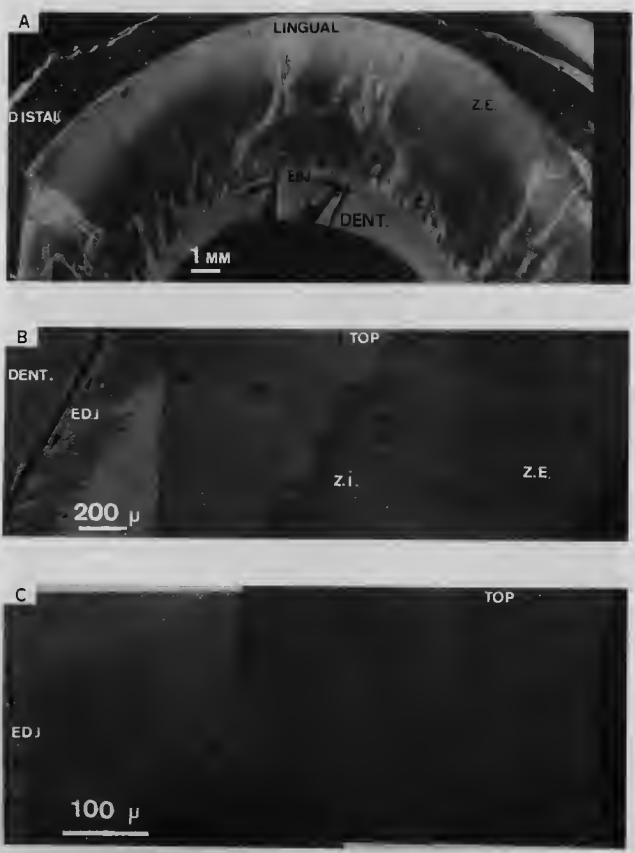
Anthracobunidae

Les deux formes étudiées sont *Jozaria palustris* (début de l'Eocéne moyen), et *Lammidhania wardi* (Eocène moyen), décrit par Wells & Gingerich (1983). Il est difficile d'apprécier la répartition des bandes de Hunter-Schreger dans la dent en raison de la taille de l'échantillon ; cependant l'émail, jamais décrit antérieurement, est organisé suivant le schéma typique (Fig. 6C) :

— Type 1 prés de la limite EDJ.
— Type 3 dans l'épaisseur de l'émail,
— Type 1 á la périphérie.

De plus les prismes, bien que parallèles entre eux, ne sont pas rectilignes, mais présentent des ondulations de grande amplitude, s'étendant sur

Source : MNHN, Paris



Source : MNHN, Paris

la quasi-totalité de l'épaisseur. On peut remarquer en microscopie á balayage, á la limite EDJ, des parazones et des diazones qui représentent environ 20 % de l'émail.

Discussion

L'évolution de l'émail dans ce groupe a déjá été envisagée par Kozawa (1978) ; cependant l'étude de l'ensemble des formes primitives permet d'aborder la reconstitution de l'évolution de la structure á travers les transformations morphologiques dentaires. Une forme telle que *Moeritherium* (Éocène-Oligocéne), apporte de nombreux renseignements sur l'organisation primitive de l'émail, bien que certains caractéres morphologiques dérivés (Coppens *et al.*, 1978 ; Tassy, 1982), l'écartent de toutes les formes postérieures.

A partir de la limite Éocène-Oligocéne, il coexiste, en Afrique, trois types structuraux distincts : le type Moeritheriidae, le type Barytheriidae, et le type Phiomiidae. L'origine de ces deux derniéres formes doit nécessairement être recherchée, par rapport á l'organisation de l'émail, chez des formes plus anciennes.

Le début d'une solution peut être proposé en étudiant les Anthracobunidae (Éocéne moyen), souvent classés prés des Proboscidea (Wells *et al.*, 1983), et qui présentent déjá un niveau d'organisation proche des Moeritheriidae, contrairement á la structure trés originale (primitive ?) des Sirenidae (Boyde, 1964 ; Sahni, 1985).

Les formes les plus anciennes de Siréniens (*Ishatherium*) ont, semble-t-il, déjá acquis dés l'Éocéne inférieur une structure identique (sans décussation) á celle de leurs descendants (Sahni, 1981a). On retrouve cette organisation chez un condylarthre *Protungulatum* du Crétacé supérieur (Sahni, 1981b), chez les insectivores, chiroptéres et certains reptiles mammaliens (Grine *et al.*, 1979).

Les Desmostyliens doivent par contre, ainsi que l'a suggéré Kozawa (1984), être rejetés de toute parenté directe avec les Proboscidea, leur structure étant proche de celle observée chez la majorité des ongulés : Artiodactyles, Périssodactyles.

Sous l'aspect phylogénétique, le regroupement de l'espéce *Numidotherium koholense* (Mahboubi *et al.*, 1986) de l'Éocéne inférieur d'Algérie, au sein des Barytheriidae est tout á fait supporté par la structure de l'émail. De même le regroupement des Barytheriidae et des Deinotheriidae (Mio-Pliocéne), parfois envisagé (Harris, 1978 ; Mahboubi *et al.*, 1986), est proposé ici : l'organisation de l'émail des deinothéres peut correspondre á une accentuation des caractéres structuraux de l'émail des barythéres.

L'hypothése phylogénétique la plus parcimonieuse nous fait proposer ce regroupement, mais l'absence de formes intermédiaires entre Barytheriidae (Éocéne) et Deinotheriidae (Miocéne-Pliocéne), nous empéche d'exclure définitivement une convergence morphologique et structurale entre ces deux groupes.

D'autre part les Gomphotheriidae (Miocéne), présentent une structure différente qui permet de les distinguer nettement et de les exclure d'une affinité directe avec les Deinotheriidae. Il apparaît que les genres *Phiomia* et *Paleomastodon* possédent déjá une organisation de l'émail comparable á celle des Gomphotheriidae, et peu compatible avec la structure de l'émail des Deinotheriidae, ce qui exclut probablement toute relation phylogénétique directe entre ces formes.

Fig. 6.

A, *Gomphotherium angustidens*. Spécimen n° SEP 224. Coll. Lab. Pal. Vert. Pal. Hum. Macrophotographie en lumiére incidente. Coupe horizontale au niveau cervical dans une molaire inférieure (M$_3$), premier lophe, face linguale. On remarque l'organisation en deux zones distincles : zone interne (= Z.I.) á bandes de Hunter-Schreger étroites et irréguliéres et zone externe trés épaisse (= Z.E.) á prismes parallées sans décussalion. Dent. = dentine.

B, *Paleomastodon beadnelli*. Oligocéne du Fayoum, British Museum of Natural History n° M 12073. MEB. Molaire supérieure. Coupe transversale, face linguale á mi-couronne. On observera la différence d'orientation des prismes entre la zone proche de EDJ et la zone la plus externe. PAR. = parazone, DIA. = diazone, Z.E. = zone externe, Z.I. = zone interne á bandes de Hunter-Schreger.

C, *Jozaria palustris*. GSP-UM n° 1738. Éocéne du Pakistan. MEB. Fragment de molaire. Coupe approximativement longitudinale. Il existe une légére décussation au niveau EDJ, mais la majorité de l'épaisseur est composée de prismes parallèles entre eux.

Source : MNHN, Paris

Il faut par ailleurs comparer cette évolution structurale avec celle de la morphologie dentaire. En effet, les Gomphotheriidae correspondent à un groupe très bunodonte dans lequel les contraintes sont omni-directionnelles, alors que les Barytheriidae-Deinotheriidae se sont orientés vers une lophodontie poussée, liée à une occlusion à forte composante latérale qui entraine des contraintes de cisaillement au niveau des faces mésiales et distales des dents.

La position des facettes d'usure, dans ces deux derniers groupes, est très révélatrice de la différence de mode de mastication. Aussi la structure très particulière de ces faces, à prismes très croisés (composante verticale de la décussation) est peut-être le corollaire d'un mode masticatoire donné. Les rôles peuvent être variables, mais nous suggérons que cela puisse diminuer les risques de propagation d'une cassure et augmenter la résistance au cisaillement. Les autres faces dentaires ou les dents non molarisées (incisives, canines) ne présentent pas ce développement de zones alternativement dirigées vers la bordure cervicale et la surface occlusale, bien que la structure globale de l'émail soit typique de ces deux groupes.

Au contraire, les dents des Gomphotheriidae doivent résister à l'abrasion, plus qu'à la rupture : le développement d'une épaisseur considérable d'émail, principalement d'une zone épaisse de prismes parallèles entre eux est peut-être une réponse fonctionnelle. Les études de Rensberger & von Koenigswald (1980) et Boyde (1984b), montrent les liens étroits qui existent entre orientation des prismes et résistance à l'abrasion.

Cet exemple de développement parallèle d'une structure et d'un mode masticatoire, peut être comparé à la différenciation de la structure des crêtes d'émail des molaires de *Mimomys* (von Koenigswald, 1980) suivant les contraintes masticatoires, ou bien le développement d'une décussation strictement verticale chez les rhinocéros (Fortelius, 1985 ; Rensberger *et al.*, 1980).

En résumé, cette étude a montré l'importance des variations structurales au sein de Proboscidea primitifs et l'existence de plans d'organisation des bandes de Hunter-Schreger distincts dès l'Éocène supérieur. Les données obtenues suggèrent que la structure de l'émail est liée indirectement à un mode masticatoire, plutôt qu'à un type particulier de dents.

Les Proboscidea se sont révélés être des formes excellentes pour une étude de la structure de l'émail sous un angle paléontologique, dans la mesure où ils offrent un terrain d'exploration relativement restreint mais néanmoins diversifié.

Il est à souhaiter que de nombreuses études sur la structure de l'émail des mammifères de l'Éocène, voire plus primitifs, viennent progressivement combler les trop nombreuses lacunes qui subsistent encore.

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Development of the Elephant Molar and the Evolution of its Enamel Structure

Y. KOZAWA, H. MISHIMA & T. SAKAE

ABSTRACT

The germs of the second molar tooth or fourth cheek tooth of *Elephas maximus* are studied by their histology. The germs are not yet calcified and the inner enamel epithelium, consisting of undifferentiated cuboidal cells, forms about 18 plate or dental lamella-like structures, as in the crown of a mature second molar. This suggests that the intricate crown of the elephant molar is fundamentally determined during the early bell stage, the same as the premolar in Bolk (1919).

The enamel of an *Elephas* molar shows a complicated structure, while the ancestral proboscideans possess a simple enamel pattern, that is, the enamel structure changes from simple to complex during proboscidean evolution. It may be considered that this structural change corresponds to the increase of enamel surface and of masticatory strength in the molar; therefore it can be said that the enamel structure is associated with the morphologic evolution of the molar.

RÉSUMÉ

Les germes de la seconde molaire (ou quatrième dent jugale) d'*Elephas maximus* sont étudiés par l'histologie. Ces germes n'ont pas atteint le stade de calcification, et l'épithélium interne de l'émail, consistant en cellules cuboïdes indifférenciées, forme environ 18 structures dentaires d'allure lamellaire comme sur la couronne de la seconde molaire adulte. Ceci suggère que la couronne complexe de la molaire d'éléphant est déterminée pour l'essentiel durant le stade précoce en cloche, comme c'est le cas pour la prémolaire (Bolk, 1919).

L'émail d'une molaire d'éléphant montre une structure compliquée, tandis que le proboscidien ancestral possède un dessin simplifié de l'émail ; la structure de l'émail évolue donc du simple au complexe durant l'évolution des Proboscidiens. On peut admettre que ce changement structural correspond à un accroissement de la surface de l'émail et un accroissement de la force masticatrice de la molaire ; par conséquent on peut dire que la structure de l'émail est associée au changement de forme de la molaire.

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Introduction

The molar of recent elephants is characterized by its large size and its very complex form. For example, the mesio-distal length is about 15 cm in the third molar of the Indian elephant. The lamellae corresponding to the cusps are about 18 in the third molar of the Indian elephant. The tooth crown is completely covered with coronal cementum, and the complex enamel ring form is the result of attrition. On the other hand, the ancestral Proboscidean, *Palaeomastodon*, has more simple molars than the recent elephant. The authors wish to demonstrate the correlation between the evolution of molar form and its histo- and cytological aspect, and to determine the ontogenetic stage at which the complex molar form is established.

Results

A. *Tooth germ*

Two second molar tooth germs, about 2.5 cm long, of *Elephas maximus* Linnaeus were sectioned and stained with hematoxylin-eosine by the Masson-Goldner method.

The inner enamel epithelium forms lammella-like structures arranged from medial to distal (Fig. 1). The three dimensional reconstruction of the inner enamel epithelium also shows 18 lamellae-like structures, which consist of three main parts (Fig. 2). At the top of the lamella-like structures there are some tubers, and the most distal structure is composed of only one tuber. These are also observed in the horizontal section (Fig. 3). These structures are basically homologous to those of the mature molar crown, which is organized in many dental lamellae.

On the mature molar crown of *Elephas maximus*, the number of lamellae is as follows: DM2 6/6, DM3 10/10. DM4 14/14, M1 17-20/17-20, M2 17-20/17-20. M3 24/22-26, according to Vaufrey (1955). The 18 lamella-like structures of the tooth germs studied correspond to the second molar (M2). There are also tubers at the top of the unworn dental lamellae which are divided into three main parts. These tubers and the three main parts can be recognized on the occlusal surface as enamel rings or enamel loops as a result of attrition (Fig. 4). Early calcifying dental lamellae are constructed of only tuber structures, which are described by Tasumi (1964) as finger-like digitelli structures (Fig. 5). These digitelli fuse and form three main parts of the dental lamellae during the progress of calcification. The dental lamellae of the molar teeth in Fig. 5 (from Tasumi, 1964) already have three main parts and tubers, the so-called digitelli. These forms are also identical to the lamellae-like structures on uncalcified tooth germs (Fig. 2).

The number of dental lamellae of the *Elephas maximus* second molar, which is 17-20 in every case (upper and lower), and their basic form

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Fig. 1. — Sagittal section of an *Elephas maximus* tooth germ by Masson-Golder staining. 18 lamellae-like structures are observed. The medial ones are larger than the distal. This tooth germ represents the second molar before the calcification stage. The number of lamellae-like structures is equivalent to that of the mature molar. This suggests that the number of dental lamellae is determined before calcification. M: medial; D: distal.

Fig. 2. — Three-dimensional reconstruction of the inner enamel epithelium of the 2nd molar tooth germ (*Elephas maximus*). Each lamella-like structure is constructed of three parts (star) and has tubers on the margin (arrow). These structures are similar to the dental lamellae of the mature molar, as suggested in Figs. 4, 5. M: medial; D: distal.

Fig. 3. — Horizontal section of the 2nd molar tooth germ by hematoxylin-eosin staining. Many rings, which are observed on the distal side, represent the margin of lamellae-like structures forming the tubers or 'digitelli' shown in Fig. 2. M: medial; D: distal.

Fig. 4. — Occlusal surface of the 2nd molar of *Elephas maximus*. The enamel loops (star) show that the dental lamella consists of three main parts and the enamel rings (arrow) show that the margin of each lamella forms the dent or the digitelli structure as was shown in Figs. 2, 3, 5. M: medial; D: distal.

Fig. 5. — Developing and calcifying dental lamellae of the 4th premolar of *Elephas maximus* from Tasumi, 1964. A is an upper and B is a lower molar lamella, both lamellae show three main parts (I-III) and digitelli structures (arrow). These structures fundamentally resemble the undifferentiated inner enamel epithelium of the bell stage in Fig. 2, 3.

Fig. 6. — Part of a tooth germ with hematoxylin-eosin staining. The inner enamel epithelium (I) and the dental papilla cells (P) do not differentiate into ameloblasts and odontoblasts respectively. The intermediate reticulum and stellate reticulum cells are observed, so that this tooth germ is in the early bell stage.

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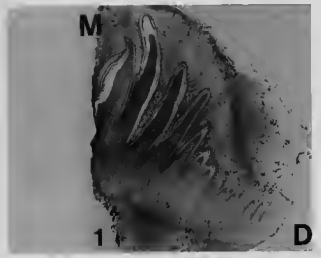

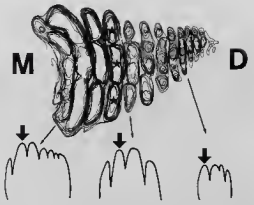

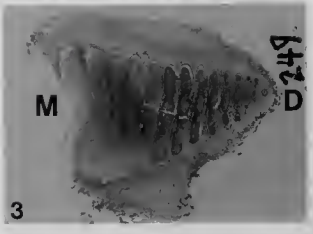

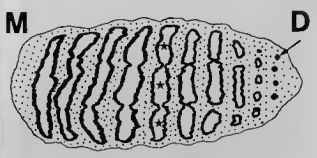

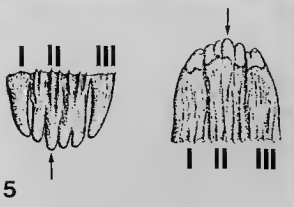

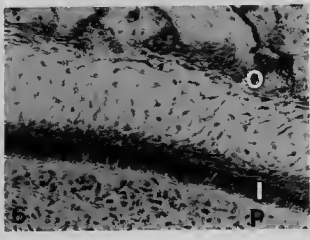

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corresponds to the lamellae-like structures of the inner enamel epithelium of these germs.

The developmental stage of these tooth germs is equivalent in histological appearance to the cap or early bell stage in the human tooth germ. This is because the inner enamel epithelium cells of the most medial side are cuboidal and the nuclei are situated at the center of the cytoplasm (Fig. 6). These cells are not mature ameloblasts and this stage is homologous to the inner enamel epithelium of the late cap stage or early bell stage of the tooth germ in human teeth. On the other hand, the cells of the dental papilla are still undifferentiated into odontoblasts on the opposite side of the inner enamel epithelium, while the stellate reticulum and intermediate reticulum cells are already present (Fig. 6).

It is suggested that the undifferentiated and uncalcified tooth germ, the early bell stage, already announces and determines the fundamental shape of the complicated form of the mature *Elephas* molar while these tooth germs are in the process of differentiation.

B. *Evolution of enamel structure*

The enamel of the Elephantidae including *Elephas maximus*, shows a more specialized structure than other mammalian enamel, as does the molar pattern (Shobusawa, 1952; Kawai, 1955; Kozawa, 1978, 1985). However, *Moeritherium* (Figs. 7 and 8) and *Palaeomastodon* (Figs. 9 and 10) have relatively simplified enamel structure. Hunter-Schreger bands are slightly curved and are arranged in an orderly manner in the enamel. The enamel prism pattern is arched, with a diameter of about 5-6 μm, and with an alternate arrangement. *Gomphotherium* and *Mastodon* have very thick enamel of about 10 mm (maximum), but its structure is similar to that of *Palaeomastodon* (Figs. 11 and 12). Hunter-Schreger bands run in an orderly fashion and the width of the dia- and para-zones is wider than in *Palaeomastodon*. The pattern of enamel prisms is the same as in the two ancestral proboscideans.

Stegodon has a complicated molar morphology, with about 10 dental lamellae, and the crown is covered with coronal cementum. The enamel structure shows the transitional pattern to that of the Elephantidae. Hunter-Schreger bands are visible but are of a quite complicated pattern, because the dia- and para-zones are confused and indistinguishable in the inner enamel layer (Fig. 13). The arched pattern of enamel prisms is commonly observed, but ginko tree leaf types can be found in some areas (Fig. 14).

The enamel structure of the Elephantidae molar is a quite special one in Mammalia (Kozawa, 1985). The enamel shows obvious Hunter-Schreger bands, but the dia- and para-zones are indistinguishable (Fig. 15). The enamel surface, the so-called enamel-coronal cementum junction, forms a rugged plane. Enamel prisms present the ginko-leaf pattern, about 7 μm wide in the middle enamel layer (Fig. 16). On the developing enamel surface can be observed (Fig. 17) many Tomes' process pits, with two dents in each pit. The two wings of the ginko-leaf pattern may be formed by this pair of dents, that is, the ginko-leaf pattern is made up of the specialized Tomes' process, which has two dents. This enamel prism pattern may be one of the largest and most complicated in eutherian Mammalia. These structures may be the result of adaptation to an increase of the enamel surface during evolution, producing an increase of enamel strength for mastication; this and the increase of the number of ameloblasts can be interpreted as a response to the herbivorous food habit. The change of enamel structure occurred along with the complication of molar form during the evolution of Proboscidea.

FIG. 7. — Hunter-Schreger bands of *Moeritherium*. The bands are slighily curved. The enamel thickness is about 1.5 mm.

FIG. 8. — Enamel prisms of *Moeritherium* are arched and arranged alternately.

FIG. 9. — Hunter-Schreger bands of *Palaeomastodon*. This pattern is similar to that of *Moeritherium*, but the enamel thickness is about 2 mm.

FIG. 10. — Enamel prisms of *Palaeomastodon* show the arched pattern and are arranged alternately.

FIG. 11. — Hunter-Schreger bands of *Gomphotherium* run in an orderly fashion in the thick enamel (about 10 mm) and the width of the dia- and para-zones is greater than that in *Palaeomastodon*.

FIG. 12. — Enamel prisms of *Gomphotherium* show the arched pattern, but their width, about 6-7 μm, is greater than that in *Palaeomastodon*. (Figs. 7, 9, 11 are sagittal sections, Figs. 8, 10, 12 are horizontal sections).

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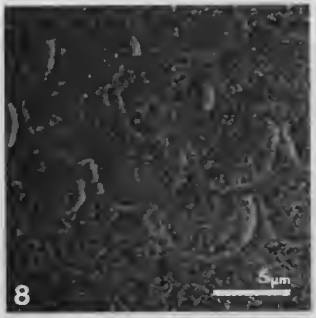

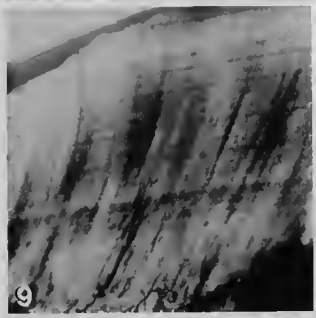

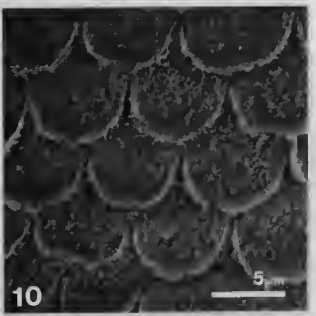

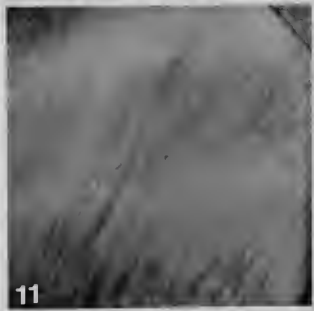

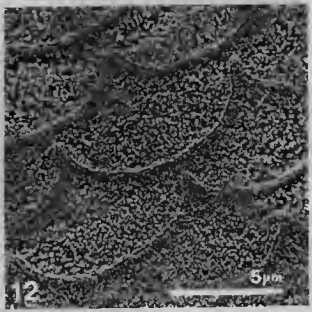

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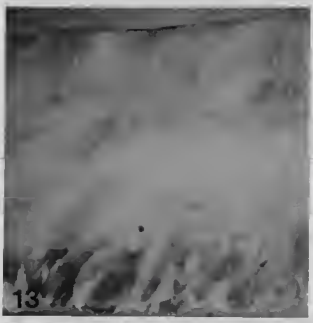

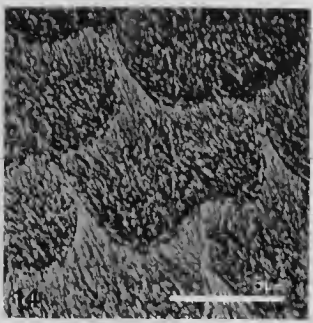

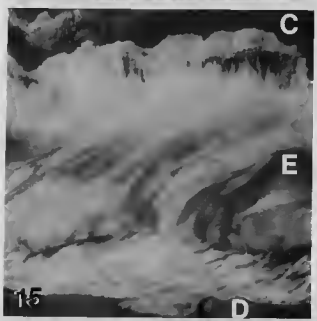

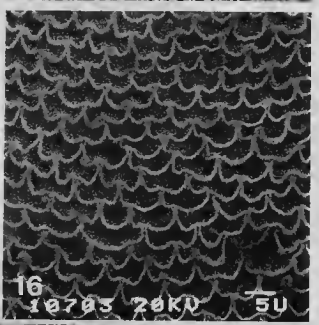

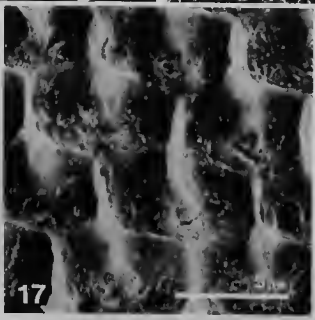

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Conclusion

The pattern of enamel prisms changed from the arched form to the ginko-leaf pattern during the evolution of Proboscidea. This change includes not only the form but also the size of enamel prisms. The latter modifications result in a change of enamel architecture and an increase of enamel surface which is an adaptation to abrasion. Hunter-Schreger bands are systematically developed in ancient, but have a more complicated pattern in modern Proboscidea. The complex Hunter-Schreger bands are characteristic of the modern elephant among Mammalia. These features are related to the molar form, development and complexity. The large and complex molar form, with a diameter over 15 cm in a mature second molar, is already determined in a small, about 2.5 cm molar tooth germ, that is, before the calcification stage.

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Fig. 13. — Hunter-Schreger bands of *Stegodon* can be clearly observed, but dia- and para-zones cannot be distinguished in the inner enamel layer.

Fig. 14. — The ginko tree leaf pattern of an enamel prism of *Stegodon*. The arched pattern is commonly observed, but this pattern can be found only in some areas.

Fig. 15. — Hunter-Schreger bands of *Palaeoloxodon naumanni*. Dia- and para-zones are not distinguishable. The enamel surface, which is the junction between the enamel and the coronal cementum (C), forms a rough plane. E: enamel; D: dentine.

Fig. 16. — The ginko tree leaf pattern of enamel prisms of *Palaeoloxodon naumanni*. This pattern is commonly observed in the middle enamel layer of Elephantidae. The width is about 7 μm.

Fig. 17. — The developing surface of enamel in the *Elephas maximus* molar. Every pit of Tomes' process has two dents, which form the two wings of the ginko tree leaf pattern of the enamel prism. These pits show that the Tomes' process of the ameloblast has two dents (Figs. 13, 15 are sagittal sections, Figs. 14, 16 are horizontal sections).

Source : MNHN, Paris

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Structural Reinforcement and Crack Propagation in Enamel

H.-U. PFRETZSCHNER

ABSTRACT

Starting with three basic mechanical assumptions, a theoretical model of the material-behaviour of enamel-like materials is developed. The model shows the critical loading conditions as well as possibilities of structural reinforcement. Mathematical calculations of the general stress pattern on the tooth surface characterize the orientation and distribution of critical stress factors on the tooth crown during chewing action. Comparison of the theoretical model with the biological microstructure of enamel shows several coincidences. Additionally, a crack stopping mechanism is demonstrated by the observation of artificial cracks in thin sections of enamel. Both the structural reinforcement and the crack stopping mechanism work in a horizontal plane. The mathematical analysis of the stress situation demonstrates the horizontal tension forces as the most critical ones. As the result of this analysis it seems highly probable that the Hunter-Schreger bands strengthen the enamel and can be interpreted as structural adaptations to the stress pattern in conical teeth and multicuspid teeth.

RÉSUMÉ

En partant de trois suppositions mécaniques de base, l'auteur développe un modèle théorique de comportement mécanique des matériaux de type adamantin. Le modèle montre les conditions de charge critique aussi bien que les possibilités de renforcement structural. Des calculs mathématiques portant sur la répartition des forces de pression exercées sur la surface dentaire caractérisent l'orientation et la répartition des facteurs critiques des pressions sur la couronne dentaire durant la mastication. La comparaison du modèle théorique avec la microstructure biologique de l'émail montre plusieurs coincidences. En outre l'existence d'un mécanisme d'arrêt de la fissuration est démontrée par l'observation de fissures artificielles dans des lames minces d'émail. Les deux phénomènes, renforcement structural et mécanisme d'arrêt de la fissuration, s'exercent dans un plan horizontal. L'analyse mathémathique de la situation de pression démontre que les forces de tension horizontales sont les plus critiques. En conclusion de cette analyse, il semble hautement probable que les bandes de Hunter-Schreger renforcent l'émail et puissent être interprétées comme des adaptations structurales aux modes de pressions exercées sur les dents coniques et les dents multicuspidées.

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Introduction

Hunter-Schreger bands are a widespread structure in mammalian teeth (Kawai, 1955; von Koenigswald, 1980). The question arises, whether the Hunter-Schreger bands are mechanically important or not, and if they are, what their mechanical function is. An early hypothesis to these questions was offered by Lehner & Plenk in 1936, but it is necessary to elaborate the theoretical background into a more precise model that can be proved by observation. In this paper I will present a theoretical model, which is deduced from a few basic mechanical assumptions. The model demonstrates critical situations for an enamel-like material as well as the possibilities of structural reinforcement. A final comparison with the observed microstructure of enamel shows several coincidences.

Observations

A. *The mechanical behaviour of an enamel-like material*

Enamel is built up of densely packed fibres; the prisms of hydroxy-apatite are held together by the interprismatic matrix, which is of the same chemical composition but differs from the prism material by a less compact packing of the submicroscopical crystallites (Keil, 1986). It is obvious that a material like this shows a fairly anisotropic mechanical behaviour. Therefore, to find the most critical situation, it is necessary to discuss not only the different types of loading — tension, compression — but also to consider the direction of the applied forces with respect to the fibre direction.

A material built up of densely packed fibres holds compression perpendicular as well as parallel to the fibre direction, because dense packing prevents the single fibres from buckling. Under tension parallel to the fibre direction the fibres accept comparatively high loading without any effect. The material easily fails under tension perpendicular to the fibre direction (Fig. 1). In this critical situation the brittle matrix has to carry the main load and the reinforcement by the fibres does not work.

This material behaviour can be traced back to three basic assumptions :

— firstly, the tensile strength of the fibres exceeds the tensile strength of the matrix. This assumption is confirmed by the compactness of the enamel prisms as well as the interprismatic growth of cracks that Boyde (1976) described (Fig. 2);

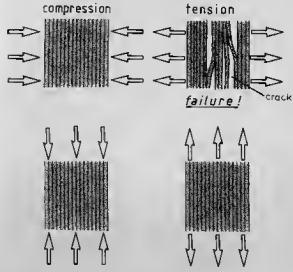

FIG. 1. — Compound material under different loading conditions.

The dense packing prevents single fibres from buckling under compression, perpendicular as well as parallel to the fibre direction. Under tension parallel to the fibre direction the material carries high loading. The material fails easily under tension perpendicular to the fibre direction. This material behaviour is caused by three basic mechanical features, cited in the picture. E = Young's modulus of elasticity.

Source : MNHN, Paris

FIG. 2. — Tangential thin section of the enamel of a canine of a dog.
The cracks, caused by the grinding process, grow interprismatically.

— secondly, the compressive strength of the matrix exceeds its tensile strength. This is obvious, because minute cracks, known as Griffith cracks, are always present and are opened only by tension forces. Under compression they make no effect (Gordon, 1984);

— thirdly, the stiffness of the prisms is higher than the stiffness of the matrix. Rigidity of the material is indicated by Young's modulus E; E of the prisms is higher than or equal to E of the matrix. This assumption is also confirmed by the observation of interprismatical growth of cracks.

The higher tensile strength of fibres is the key to structural reinforcement of the material.

B. *Structural reinforcement of compound materials*

Material failure can be prevented by the arrangement of several layers of different fibre directions in the plane in which the force acts. We distinguish carrying layers from reinforced layers. The carrying layers contain fibres in the force direction. They carry the main part of the load, because the Young's modulus of the prisms is assumed to be higher than the Young's modulus of the matrix. In this way they support the adjacent layers. Does the thickness of the layers have any effect in this context? In two materials, both built up by layers of crossed fibre direction but differing in the thickness of the layers, the maximum tensile strength of both materials is the same, because the sum of the cross sections of the carrying layers is the same (Fig. 3).

The carrying layers only can reinforce the adjacent layers if force is transmitted from one layer to the other. At a given maximum force per unit area, the reinforcement is better in the case of the thin layers, because the junction area is larger than it is in the other case (Fig. 3).

In other words: better reinforcement at the same maximum tensile strength is achieved by decreasing thickness of the layers.

C. *Statics of the tooth crown*

If tension forces acting perpendicular to the fibres is the most critical situation, the question arises whether there are any tension forces

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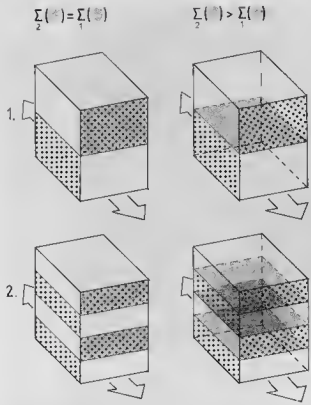

FIG. 3. — Two compound materials with differing thickness of the layers.

In the left part of the picture the carrying layers are hatched. Both materials possess the same portion of carrying layers (equation at the top). Therefore the maximum tensile strength is the same in both materials. In the right part of the picture the junction areas between the adjacent layers are hatched. In the case of thin layers the sum of the junction areas exceeds that of the upper example. Reinforcement is better in the lower example. The light arrows indicate the direction in which the tension force acts.

present during normal chewing action. The answer is given by calculations of the stress pattern on the tooth. These calculations can be carried out by means of shell theory, a mathematical theory that is used in engineering and in architecture (W. Flügge, 1981; A. Pflüger, 1981). The enamel can be approached as a thin shell, because it is 3 to 4 times less elastic than dentine. As a simple model a unicuspid conical tooth is chosen, as in canines of several carnivores, but the principle is the same in more complex teeth, like multicuspid and bunodont molars.

Simple geometrical models are the rotatory ellipsoid and the elliptic ellipsoid (Fig. 4). The dentine is calculated as hydrostatic pressure in reaction to the applied load.

The results of the calculations are sketched in Fig. 5. " Snow load " is the technical term for constant pressure referring to the horizontal plane. The calculations show tension forces occurring in the horizontal plane with a maximum at the base of the crown.

The second loading type is the " wind load " as an example for an asymmetric load. The calculations show tension forces occurring only

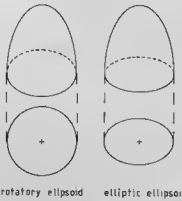

FIG. 4. — Outward appearance and cross sections of mathematical defined shell types.

on one side of the tooth. On the opposite side of the tooth only compressive forces occur. As it is shown in the diagramm, the vertical tension forces are 0 at the tip as well as on the base of the crown, with a maximum in between. However, the horizontal tension forces are always higher than the vertical tension forces, if the tooth is not too slender. The maximum horizontal tension forces appear again at the base of the crown.

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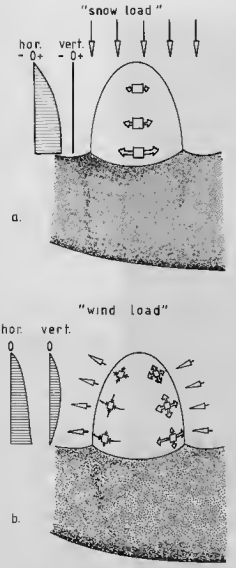

FIG. 5. — Results of the calculations of the stress pattern.
a, Snow load = constant load with respect to the horizontal plane. Dark arrows: compressive forces; light arrows: tension forces. The diagram at the left shows the values and the sign of the forces. + = tension, — = compression.
b, Wind load = asymmetric load; there are no signs on the diagram, because all the forces are compressive at the left side of the tooth and tension forces at the right side.

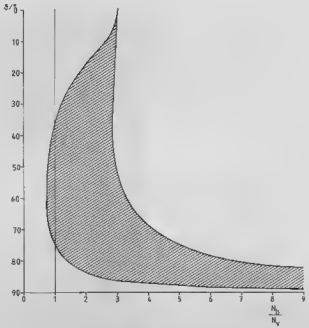

FIG. 6. — The ratio of the horizontal tension forces N_h to the vertical tension forces N_v as a function of the inclination of the normal vector of the shell with respect to the vertical direction. Hatched area: curves of different slenderness of the canines. The values of the slenderness (crown height/diameter of the crown at the base) are measured for the following species: *Panthera tigris, P. leo, P. unica, Leopardus pardus, Felis concolor, Crocuta crocuta, Melursus ursinus, Thalassarctos maritimus, Ursus arctos, Otaria bryonia, Protocephalus pusillus, Zalophus californicus.*

What does " too slender " mean? Fig. 6 shows the quotient horizontal tension force/vertical tension force as function of the inclination of the normal vector of the shell surface with respect to the vertical direction. The two curves that indicate the margin of the hatched area are due to two extreme values of slenderness (= index: height of the crown: diameter of the crown base in the direction of force application) which were measured in 12 different species of large carnivores. The curves of the ten remaining species lay in the hatched area, which can be interpreted as the biological relevant range.

Only a very small part of the area reaches values smaller than 1, meaning the vertical forces are higher than the horizontal forces.

Summarized: in both situations tension forces exist. They act in a horizontal plane and reach maximum values at the base of the crown.

D. *Crack distribution on teeth and structural coincidences with the mechanical model*

Examination of canines and premolars show that if cracks appear, most of them are vertically

Source : MNHN, Paris

oriented and lie at the base of the crown (Figs. 8 and 9). This can be expected from the results of the calculations above. Only in slender canines may some horizontal cracks appear half way up to the tip of the crown, due to the local maximum of vertical tension forces under " wind load ". But this happens only to slender canines.

This crack distribution corroborates the former calculations as well as their biological importance.

Reinforcement of the enamel with respect to these tension forces requires horizontal layers with decussated fibres. That is what Hunter-Schreger bands are (Fig. 7). Since reinforcement is a function of the thickness of the layers, we would expect only small size variations of Hunter-Schreger bands in one species. The data published by Kawai (1955) as well as the data shown in Fig. 10 confirm the expectation. The thickness was measured on ground sections under the light microscope. Each diagram shows the distribution of the thickness of Hunter-Schreger bands in one species. There are only small variations, caused mainly by the bifurcations of the Hunter-Schreger bands, as they are shown in Fig. 7.

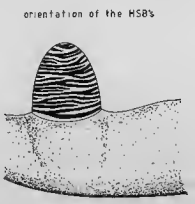

FIG. 7. — Orientation of the HSB's on the tooth.

Additionally, in the case of higher loading we find decreasing thickness of the Hunter-Schreger bands, as it is shown in Fig. 10 for the chisel-like incisors of the primate *Daubentonia madagascariensis*. The maximum is shifted to smaller values. Several examples of Hunter-Schreger bands with extremely reduced thickness are found in modern rodents by reduction to single prism layers in the " Lamellenschmelz " (von Koenigswald, 1980).

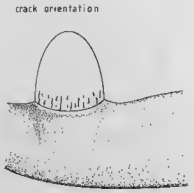

FIG. 8. — Crack distribution on the crown.

E. *Crack propagation and crack stopping*

Up to now I have discussed the reinforcement, which means the prevention of crack formation. But what happens to cracks that already exist during loading? As I stated above, minute cracks are always present.

If the matrix has a lower tensile strength and is more elastic than the fibres, the cracks should grow in between the prisms. This is already described by Boyde (1976) and can be easily observed by the light microscope (Fig. 2) or by the SEM.

In Fig. 11a a model of the enamel with Hunter-Schreger bands and horizontal decussated prisms is shown. For clearness, the Hunter-Schreger bands are only two prism layers thick, but the principle is the same for thicker Hunter-Schreger bands. Horizontal cracks, caused by vertical forces (Fig. 11c), run straight through the enamel until they reach the dentine-enamel junction. But vertical cracks (Fig. 11b), caused by the more important horizontal forces, will turn to the right or to the left, as the prisms do. They will stop soon, because they are inclined with respect to the force direction.

In thin section, several cracks can be caused by the grinding process. As is to be expected we find straight cracks that run through the whole thickness of the enamel in vertical thin sections. In horizontal sections we find curved and divided cracks (typical Y-shaped) that stop in the enamel in most cases (Figs. 12 and 13). This is the

Source : MNHN, Paris

FIG. 9. — Vertical cracks at the base of the crown of a canine of *Leopardus pardus*.

biological more important case, as I stated above. Indeed, crack propagation agrees with our model and prism decussation acts as a crack stopping mechanism with respect to horizontal tension forces.

DISCUSSION

The Hunter-Schreger bands show several structural coincidences with the theoretical model for structural reinforcement. They are layers with decussated fibres; the thickness of the Hunter-Schreger bands varies only to a small degree and decrease during evolution in cases of high loading (incisors of rodents, von Koenigswald, 1980). The prism decussation additionally works as a crack stopping mechanism, as is shown by the propagation of artificial cracks. It seems obvious that the Hunter-Schreger bands possess all features necessary to reinforce the enamel with respect to the forces during chewing action. A mechanical adaptation during evolution can only appear due to a certain stress factor that is the same in all the different loading types. A structural adaptation to vertical compression during snow load and to vertical tension during wind load is impossible. The horizontal tension forces are shown to be present in the different loading types, to be the most critical stress factor, to be

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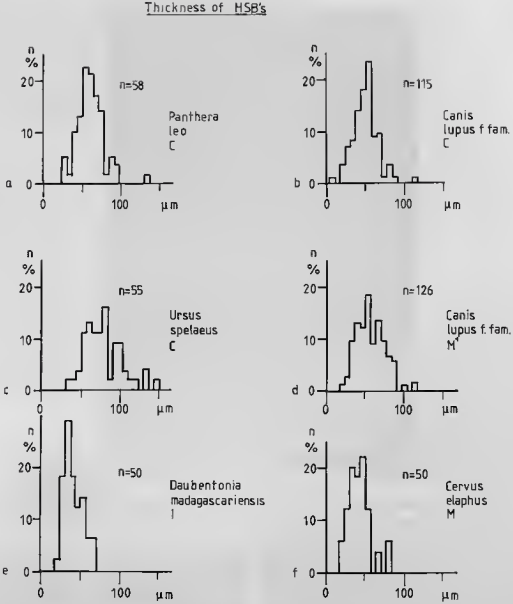

FIG. 10. — Distribution of the thickness of HSB's in different species, measured on ground sections under the light microscope; n = number of the measured HSB's.

the largest tension forces that occur and to possess a maximum at the base of the crown. Indeed the Hunter-Schreger bands strengthen the material in the horizontal plane with respect to tension forces by structural reinforcement and crack stopping. During evolution they appear initially at the base of the crown (von Koenigswald, Rensberger & Pfretzschner, 1987; von Koenigswald & Pfretzschner, 1987). Therefore, the Hunter-Schreger bands possess several features of a structural adaptation in response to the sole stress factor; this is due to very different loading types of a cone-shaped tooth crown, essentially a cusp on a crown.

In the case of highly specialized teeth due to a different and perhaps much more strictly defined loading type (single loading type!), as in the molars of several herbivores, other structural

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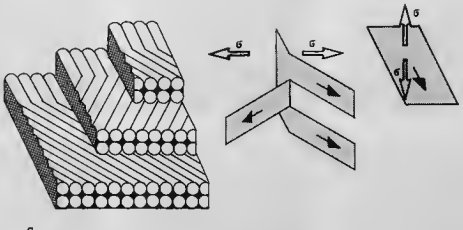

FIG. 11. —
a, Model of enamel with HSB's.
b, Vertical cracks running into the enamel. The cracks turn to the right or to the left just as the prisms do. In the transmitting light microscope one can see a typical Y-shaped crack. It will stop soon, because it is inclined to the force direction.
c, Horizontal crack runs straight through the whole enamel.

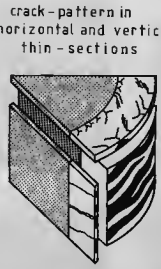

FIG. 12. — Crack patterns in horizontal and vertical thin sections of teeth. Hatched area: dentine. The cracks in the vertical sections run straight through the enamel. The cracks in the horizontal sections are curved, typical Y-shaped and stop in the enamel.

adaptation may be more successful. Indeed the Hunter-Schreger bands often are varied to a high degree in these cases.

Finally, it seems obvious that the Hunter-Schreger bands are an evolutionary adaptation reinforcing the enamel in cone-shaped teeth under greatly varying loading conditions.

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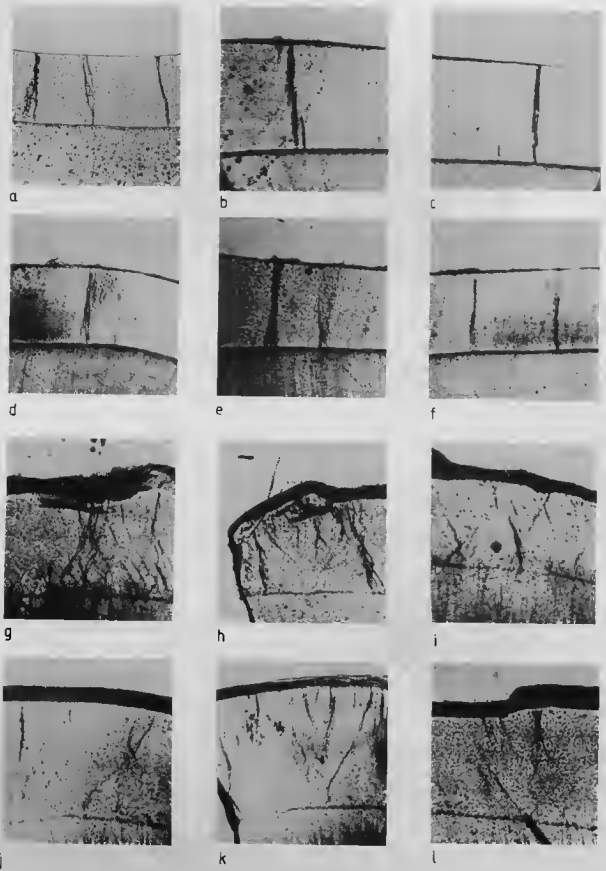

FIG. 13. — Propagation of artificial cracks in thin sections.
a-f, vertical sections. Straight cracks.
g-l, horizontal sections. Curved, typical Y-shaped and splitted cracks. Most of them stop in the enamel.

Source : MNHN, Paris

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Enamel Modification in Enlarged Front Teeth among Mammals and the Various Possible Reinforcements of the Enamel

W. von KOENIGSWALD

ABSTRACT

Several mammals, not only rodents, develop enlarged front teeth, which are only partially covered by enamel. They form sharp cutting edges during abrasion. The Schmelzmuster (microstructure of the enamel) in these teeth differs frequently from the remaining teeth of the same dentition. The differences in the Schmelzmuster demonstrate adaptations to different biomechanical requirements. To avoid or to stop cracks is one of the main characters of these structures. Besides the underived radial enamel three different enamel types are present:

1. simultaneous turn of prisms, where all prisms stay in parallel;

2. Hunter-Schreger bands, where prisms arranged in layers cross over each other;

3. interweaving bundles of prisms.

These are general structures that reinforce the enamel. They are found in molar dentitions too. A fourth enamel type, however, where single prisms cross over each other, as in Lemming enamel, is found in molars but so far not in enlarged front teeth.

RÉSUMÉ

De nombreux Mammifères, et pas seulement les Rongeurs, présentent des dents antérieures particulièrement développées, qui ne sont que partiellement recouvertes d'émail. L'abrasion aiguise le bord coupant de ces dents. Sur celles-ci, la microstructure de l'émail diffère fréquemment de ce qu'elle est sur les autres éléments de la même denture. Ces différences de microstructure témoignent d'adaptations à des contraintes biomécaniques différentes. Un des principaux caractères de ces structures est d'éviter ou d'arrêter la fissuration. A côté de l'émail radiaire primitif, on trouve trois autres types d'émail :

1. inclinaison simultanée des prismes, qui restent parallèles les uns aux autres ;

2. bandes de Hunter-Schreger, où les prismes disposés en couches se croisent les uns les autres ;

3. paquets de prismes qui s'entrecroisent.

Ces structures ont pour effet de renforcer l'émail. On les trouve également sur des molaires. Un quatrième type d'émail, cependant, où ce sont les prismes pris isolément qui s'entrecroisent, comme chez le Lemming, a été observé sur des molaires mais pas, jusqu'ici, sur les dents antérieures de grande taille.

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Zusammenfassung

Zahlreiche Säugetiere, nicht nur Nager, haben vergrößerte Vorderzähne entwickelt, die nur teilweise mit Schmelz bedeckt sind. Durch den Abrieb bildet der Schmelz eine scharfe Schneidekante. Das Schmelzmuster (interne Struktur des Schmelzes) unterschidet sich bei diesen Zähnen häufig von dem der übrigen Zähne im gleichen Gebiß. Der Unterschied in dem Schmelzmuster zeigt die Anpassung an unterschiedliche biomechanische Erfordernisse. Risse im Schmelz zu verhindern oder aufzuhalten, ist eine der Hauptaufgaben dieser Strukturen. Außer dem undifferenzierten radialen Schmelz können drei Schmelztypen unterschieden werden:

1. gleichsinniges Abknicken der Prismen, die dabei untereinander parallel bleiben;
2. Hunter-Schreger-Bänder, in denen sich die Prismen lagenweise überkreuzen;
3. Prismenbündel, die sich überkreuzen.

Es handelt sich dabei um grundsätzliche Strukturen zur Verstärkung des Schmelzes, die auch in anderen Zahntypen gefunden werden können. Ein weiterer Schmelztyp, in dem sich Prismen überkreuzen, wie im Lemming-Schmelz, wurde zwar in verschiedenen Nagetiermolaren gefunden, nicht jedoch in den vergrößerten Vorderzähnen.

Introduction

Many studies, devoted solely to the enamel of rodent incisors and the use of terms like " rodent enamel ", suggest that all rodent teeth, including the cheek, show one particular type of enamel. Certainly this is incorrect. Little is known, however, about the relationship of the enamel structure of incisors to that in molars of the same dentition.

A survey devoted to this relationship should not concentrate on rodents although the enamel structure of their incisors has been studied in great detail (Tomes, 1850; Korvenkontio, 1934; Wahlert, 1968; von Koenigswald, 1985). In many rodents the molars also underwent independent differentiation which changed the enamel (von Koenigswald, 1980); the comparison of incisors and molars is complicated, and general tendencies may be obliterated; to obtain a picture of more general value this survey covers quite a number of enlarged teeth from various mammalian orders. Several fossil forms can be added to the convergences listed by Moeller (1974). This study is not restricted to such close convergences but incorporates other enlarged front teeth like the canines of *Hippopotamus* and the incisors of rhinoceroses.

In addition to these teeth which function similary to rodent incisors, some enlarged incisors of insectivores and other " primitive " mammals are examined in order to cover a wider range of enamel structures.

On the other hand, enlarged canines of carnivores were excluded, since they are surrounded by enamel, and, according to the present stage of my knowledge, they do not contribute relevant information. Some other taxa like extant elephants or walruses enlarged their front teeth but reduced the enamel completely, so that they can be omitted here.

The enamel of the enlarged front teeth will be compared with the enamel in the cheek teeth of the same species. A survey based on such a wide range of material promises to show general tendencies such as the front teeth must be enlarged to need a specific reinforcement of the enamel and whether there are different ways to reinforce the enamel. The chance of finding such structures is fairly high, since these enlarged teeth are exposed to high stresses. Reinforcing structures may differ, since enlarged front teeth were developed several times in parallel.

The study concentrated on teeth that are covered with enamel on one side only. This character is usually associated with hypsodonty, and in many cases the teeth grow continuously. A high extrusion rate is compensated by high attrition, and a result of the difference in hardness between enamel and dentine, the enamel forms a sharp cutting edge.

Strengthening in the enamel is needed since the greater forces tend to destroy the enamel by cracks; most reinforcing structures can be interpreted in the sense of stopping crack propagation as Lehner & Plenk (1936) have argued for Hunter-Schreger bands.

Source : MNHN, Paris

Material and Method

The techniques applied in enamel studies differ according to the point of interest. This paper takes a biomechanical approach and concentrates on the course of the prisms throughout the enamel. The regular course of the prisms within a restricted area defines the enamel type, e.g., radial enamel, Hunter-Schreger bands, etc. (von Koenigswald, 1980).

The three dimensional arrangement of different enamel types is called Schmelzmuster. It may be closely related to the stress pattern of the tooth (von Koenigswald, 1980, 1982). In this study the prism cross section as studied by Boyde (1960) and Carlson & Krause (1985) and the density of prism packing (Fosse *et al.*, 1978) are of minor interest here.

The course of prisms can be determined by the use of the scanning electron microscope or the reflecting light microscope from sections ground in various directions. In both cases it is necessary to etch the surface. This usually was done for 2 to 5 sec. with 2n hydrochloric acid. Rough etching removes part of the interprismatic matrix (IPM), and eventually part of the prisms, too, but as long as the course of the prisms can be distinguished this simple method is sufficient.

Prisms are arranged commonly in thick layers such as in Hunter-Schreger bands (HSB), which are widely distributed in mammalian teeth (Kawai, 1955). Prism direction in such layers can be determined even under low magnification, since prisms act as light guides (Rensberger & von Koenigswald, 1980; von Koenigswald & Pfretzschner, in press). The extensive use of this effect allows study of material which is so rare that any damage must be avoided.

Three main orientations were used for the sections. In hypsodont teeth, studied here, the longitudinal axis is parallel to the growing axis. The transversal section is at right angles to the longitudinal one; a tangential section passes through the enamel parallel to the enamel dentine junction (EDJ).

Prisms as well as HSB may be inclined at different angles to the EDJ. The angle is measured from the EDJ (Beier, 1985), so that a low value signifies a steep inclination, while 90° is perpendicular to the EDJ and means no inclination. Normally the prisms are inclined more steeply than the HSB of the same enamel.

Measurements are given as an indication of the order of magnitude; they are not statistically derived averages. At the present state of knowledge the order of magnitude is enough to discriminate the structures of interest; a statistical treatment would require the destruction of much more material.

The aim of each description in the following section is to present the three dimensional arrangement of structures formed by enamel prisms. They were the result of the investigation of the external surface as well as of sections of different orientations and of different planes.

Abbreviations:

EDJ	Enamel-dentine junction
HSB	Hunter-Schreger bands
IPM	Interprismatic matrix
KOE 265	Number of the reference material in the enamel collection of the author

Museums which made material available:

AMNH	American Museum of Natural History, New York
BSPM	Bayer. Staatssammlung Paläontologie hist. Geologie, München
HLMD	Hessisches Landesmuseum Darmstadt
IVPP	Institute of Vertebrate Paleontology, Beijing
NHMB	Naturhistorisches Museum Basel
PMN	Paleontological Museum, Moscow
SMF	Senckenbergmuseum Frankfurt a.M.

Besides the material described here, important information on the Multituberculata was obtained from Sahni (1979), Fosse *et al.* (1978) and Carlson & Krause (1985) and on the Marsupialia from Beier (1981, 1983, 1984).

Results

Marsupialia

Macropus giganteus Shaw, 1790, *Macropus rufus* (Desmaret, 1822).

Recent, lower incisors in cross section (Figs. 3 and 4).

The lower incisors are elongated and extrude almost horizontally from the mandibule. Longitudinal ridges are formed on the upper lateral and on the lower mesial side. The enamel, seen in cross section, is two-layered; prisms are parallel

Source : MNHN, Paris

in both layers. In the inner layer, which occupies 15-20 % of the total thickness, all prisms point upwards to the upper ridge of the tooth. On a line parallel to the EDJ, prisms turn abruptly towards the anterior top of the tooth.

In the specimen studied no HSB could be identified, but Beier (1983) described and figured prism decussation, orientated vertically to the EDJ, especially for the genus *Petrogale* within the upper and lower ridges of the tooth.

Radial enamel covers these layers of decussating prisms. The layers themselves are much thinner than HSB in *Vombatus* and artiodactyls, for instance, so they cannot be observed with reflected light under low magnification.

Vombatus ursinus Shaw, 1800 and *Lasiorhinus latifrons* Owen, 1845.
Recent, upper and lower incisors and molars (KOE 265/273/274).

The upper and lower incisors, which grow continuously, are covered with enamel only on the labial side. Transversaly orientated HSB are well developed and bifurcate regularly. The HSB can be observed from the outside only after the removal of the cementum or in the alveolar part where the cementum is not yet formed. In a longitudinal section *Vombatus* has convexly curved HSB which are inclined in the inner portion at about 60° to the EDJ but tend to meet the outer surface almost perpendicularly. In *Lasiorhinus* the HSB are straighter. Their inclination measures about 45°. In both genera the HSB do not start at the EDJ but leave an inner layer of radial enamel that occupies about 25 % of the enamel thickness. The IPM tends to form inter-row sheets.

The enamel structure in molars is quite similar. The only difference occurs in the angle of inclination, as Beier (1981) demonstrated. Upper molars are covered by enamel only on the lingual side and lower molars on the labial side. In biomechanical terms the cutting edge is always on the trailing edge of the molars.

Diprotodon sp.
Pleistocene, Imp. Bingera, New South Wales; fragment of lower incisor (KOE 417).

The lower incisor of *Diprotodon*, which is continuously extruded from the jaw, is about 45 mm wide. The 1.4 mm thick enamel on the labial side forms a sharp cutting edge. Radial enamel seems to be dominant. The prisms rise apically from the EDJ with a 50° inclination but bend down gently to meet the outer surface almost perpendicularly. In the inner half of the enamel the prism direction varies in longitudinal and in transverse sections. Some prism decussation may be present here, even though it could not be observed directly. By no means do the decussating prisms form HSB. IPM forms inter-row sheets, but it anastomoses between prisms as well. It is orientated at a high angle relative to the prism direction.

Apatotheria

Heterohyus gracilis (Stehlin, 1916) and *Heterohyus europaeus* (Rütimeyer, 1890).
Eocene, Egerkingen, Switzerland; fragments of lower incisors (NHMB Eh 605 and Ef 988) — (KOE 427/426) (Fig. 1).

In this extinct group the continuously or almost continuously growing lower incisors are covered by enamel on the labial side only. The enamel thickness in *H. gracilis* is 0.4 mm and in *H. europaeus*, 0.8 mm. The prisms are almost straight and not inclined (90°). Only close to the EDJ a slight wave could be observed, but whether it bent upwards or downwards could not be distinguished from the isolated fragment.

The incisors of *Heterohyus europaeus* are similar in size to those of *Castor fiber*, but they are much more compressed laterally.

Lipotyphla

Sorex araneus L., 1758; *Neomys fodiens* (Pennant, 1771); *Crocidura leucodon* (Herrmann, 1780).
Recent, Southern Germany; several dentitions from owl pellets. (KOE 456/239) (fig. 5).

Blarina brevicaudata (Gray, 1823).
Recent, New York (KOE 227).

The lower incisors of soricids are fairly elongated but attrition is relatively slight; in general the enamel is two-layered. The difference between these two layers is characterized by a distinct turn in prism direction. Since the teeth have such

Source : MNHN, Paris

a rich morphology it is difficult to describe the prism direction. On the lateral side of the almost horizontal lower incisor, the prism direction could be determined as follows: in the inner layer the prisms point upwards to the almost horizontal edge and they are well separated by inter-row sheets; when prisms enter the outer enamel layer they turn toward the anterior tip of the tooth. This outer enamel in *Blarina*, *Sorex*, and *Neomys* is stained by iron minerals, which change the solubility in acids. This complicates the observation of the prism course. In molars a similar two-layered enamel can be observed. No prism decussation or HSB was found in soricids.

Primates

Daubentonia madagascariensis (Gmelin, 1788).
Recent, Madagascar; lower and upper incisor (SMF — 1583) — (KOE 275).

The highly oval cross section of the incisors is covered by enamel only on the lingual side. In the mesial part the enamel is about 0.6 mm thick. HSB are well developed. Basically they are orientated transversely; near the lateral margins of the enamel, however, the HSB rise toward the occlusal surface and bifurcate more often than in the mesial section where they have an extremely regular transverse orientation. In a longitudinal section, the HSB rise apically almost directly from the EDJ at an angle of 50°. The thickness of the HSB is about 7 to 9 prism cross sections; these are counted to include half of each transitional zone. The outermost part of the enamel, about 10-15 % of the thickness, is free of HSB and formed by radial enamel.

The HSB are characterized by a wide transitional zone in which the prisms change gently from one band to the next higher one (von Koenigswald & Pfretzschner, 1987).

The 1PM is organized mostly as inter-row sheets; in tangential sections an undulating lineament, as in lagomorphs, is visible.

Molars are morphologically simplified and were not sectioned, but from the outside very regular HSB, as in incisors, are visible.

Proboscidea

Tetralophodon longirostris (Kaup, 1832).
Upper Miocene, Dinotheriensande, Esselborn (Rheinhessen), fragment of incisor (HLMD Din 845, 944-946) — (KOE 455) (Fig. 6).

The tusk has only a narrow longitudinal band of enamel, which is about 1.5 mm thick. Prism decussation is present throughout the entire thickness. Prisms are not arranged in bands but in bundles that wind around each other. The structure corresponds to that of the inner layer in molar teeth.

Rhinocerotoidea

Aceratherium incisivum Kaup, 1832, and *Brachypotherium goldfussi* (Kaup, 1834).
Upper Miocene, Dinotheriensande, Eppelsheim and Wissberg; several lower incisors (HLMD — Din 1867, 1873, 1883) and molars.

Prosantorhinus germanicus (Wang, 1929).
Upper Miocene, Sandelzhausen, Bavaria; fragment of incisor, (BSPM) — (KOE 452).

The enamel of the incisor is about 1 mm thick and forms a sharp cutting edge. HSB penetrate the entire thickness of the enamel and are transversely orientated. In molars the enamel has two layers. Under a thick radial enamel the inner part shows HSB in vertical arrangement (Rensberger & von Koenigswald, 1980).

Indricotherium transouralicum Pavlova, 1923.
Oligocene, Chelkar-Teniz, Kazakhstan; lower jaw (PMM).

In the large cone-shaped incisors HSB are orientated transversely. In the molars vertical HSB penetrate most of the enamel thickness.

Metamynodon planifrons Scott & Osborn, 1883.
Oligocene, South Dakota; lower jaw (HLMD).

The extremely large molars have vertical HSB under a cover of radial enamel as in Rhinocerotidae (Fortelius, 1985). The enlarged canines, however, have only a thin cover of enamel, which contains tranversely orientated HSB.

Source : MNHN, Paris

Astrapotheria

Astrapothere *gen. et sp. indet.*
Coli-Huapi, Chubut, Argentinia; left upper canine from a fragmented skull (AMNH 29724).

The upper tusk is covered by enamel on the lateral and mesial side while the anterior side is free. In longitudinal sections HSB are visible in the inner layer of the enamel. In the distal part of the lateral side the HSB are transversely orientated but bent downwards close to the mesial margins of the enamel.

For the molars, which were not checked here, Fortelius (1984) described and figured vertical HSB.

Hyracoidea

Procavia capensis (Pallas, 1766).
Pleistocene, East Africa, upper and lower incisors as well as molars (KOE 277, 395) (Fig. 2).

The enamel covering the labial side of the upper incisor is extremely thin, measuring 0.1 mm. It is formed only by radial enamel. No HSB or any bending of prisms could be detected. The elongated lower incisors are surrounded by enamel but only radial enamel is found here, too.

In a section of a premolar, radial enamel dominated, but a small area close to the outer surface was detected where individual prisms change their direction and cross over each other. But they do not form HSB.

However. in an upper molar of a giant hyracoid mammal from the Oligocene of Fayum, HSB could be observed.

Notoungulata

Nesodon imbricatus Owen, 1853.
Miocene, Patagonia, upper jaw (HLMD).

The greatly enlarged upper first incisor has a triangular cross section that is covered with enamel only on the lateral and mesial sides. The enamel shows very distinctly marked HSB in transverse orientation. The HSB obviously penetrate the entire enamel thickness. In premolars and molars horizontal HSB are present as well, but they are developed only close to the EDJ.

Artiodactyla

Hippopotamus amphibius incognitus Faure, 1984.
Ipswichian, Upper Pleistocene, Lincoln England; fragments of canines (KOE 453).

Hippopotamus sp.
Pleistocene, Java; molar fragments (KOE 458).

The enamel of the canines is crenulated at the surface. Its thickness is about 0.7 mm. HSB are well developed and penetrate the entire thickness of the enamel. They are very clear at the EDJ but lose clearness at the outer surface. They are transversely orientated; in a longitudinal section the HSB decline first and change into a horizontal direction, thus forming a curve that is concave upward.

In molars the enamel is much thicker, about 2.5 mm. The HSB are less clear close to the EDJ. They are transversely orientated and inclined apically in the innermost portion but curve convexly as they pass outward to meet the outer surface at about 90°.

Lama sp.
Recent, Chile; incisors and molars (KOE 274) (Fig. 8).

The strongly hypsodont incisors are covered with enamel only on the labial side. The enamel is smooth on the outside, but the specimen studied showed growth lines at the EDJ. The enamel is about 0.8 to 0.9 mm thick. Transversely orientated HSB penetrate the enamel. In a longitudinal section the HSB are inclined apically at about 45° to the EDJ but bend convexly in the outer quarter of the enamel to meet the outer surface almost perpendicularly. The same pattern is found in molars.

Myotragus balearicus Bate, 1909.
Pleistocene, Campanet cave, Mallorca; fragment of lower incisors and molars (KOE 271).

The lower incisor is compressed and covered only on the labial side with enamel of about 0.5 mm. The outer surface is slightly crenulated. The innermost layer (10-15 %) is free of HSB, which becomes very clear in the remaining part of the enamel. The thickness of the bands is about 6 to 9 prisms in cross section. The HSB are orientated tranversely and bifurcate regularly. In

Source : MNHN, Paris

a longitudinal section the straight HSB are inclined apically at about 50° to the EDJ. IPM is mainly organized in inter-row sheets. Molars show the same structure.

Mixodontia

Rhombomylus sp.
Early to Middle Eocene, Da-jian, Xi-jia-dian, Jun-cian, Hubei province, China; lower and upper incisors and molars (V 5257 IVPP) (KOE 387).

The enamel of the incisors is only about 0.1 mm thick and, in contrast to rodents, only one-layered. HSB penetrate the entire thickness of the enamel. They are orientated tranversely, regularly bifurcating, and in a longitudinal section, inclined apically at about 70°. The IPM that surrounds the prisms does not form inter-row sheets as in Lagomorpha. The low-crowned molars show the same Schmelzmuster as the incisors and differ in this trait from the Lagomorpha, which have two layers in their cheek teeth.

Li and Ting (1985) demonstrated for the Paleocene mixodontoid *Heomys orientalis* the presence of two layers in the enamel of incisors. The HSB of the inner layer are overlain by radial enamel.

Lagomorpha

Lepus europaeus L., 1758.
Recent, Central Europe; several dentitions (KOE 10) (Fig. 9).

The enamel of the incisor is penetrated by HSB from the EDJ toward the outer surface. In a longitudinal section the transversely orientated HSB are inclined apically at about 35° to the EDJ. The thickness of the HSB is about 7 to 8 prism cross sections, so that the term "multiserial" is adequate. The IPM tends to form inter-row sheets. In tangential sections the presence of inter-row sheets creates an undulating basement since the prisms of adjacent bands are sectioned at different angles. Cheek teeth have two layers in their enamel. The inner layer has multiserial HSB, and the outer, radial enamel.

Rodentia

Hystrix.
Recent, Uganda; upper and lower dentition (KOE 25).

The enamel of the incisor is about 0.45 mm thick and has two layers. The inner one, the *portio interna*, is penetrated by multiserial HSB, which originate at the EDJ. They are orientated tranversely and are only slightly inclined in apical direction (80°). In tangential section this layer shows the undulating lineament as nicely as lagomorphs. The outer layer, the *portio externa*, is of radial enamel, which occupies about 30 % of the total thickness.

In cheek teeth the enamel is characterized by thick slightly convex HSB that curve in an apical direction. The HSB extend to the outer surface of the tooth.

Chinchilla laniger (Molina, 1782).
Recent, from breeding stocks; several dentitions (KOE 221) (Figs. 10 and 11).

In the incisors a layer of radial enamel is present between the EDJ and the HSB of the *portio interna*. It can be as much as 10 to 15 % of the enamel thickness. The HSB are orientated transversely and bifurcate frequently but very regularly. In a longitudinal section the HSB bifurcate so often that the apical inclination can be hidden. Each HSB is of about 5 prisms that quickly penetrate from one HSB into the next higher. Very similar pictures may be obtained from *Daubentonia*. The HSB fade out into the outer radial enamel, which occupies about 20-25 % of the enamel thickness.

In the cheek teeth the enamel is reduced on the leading edge (von Koenigswald, 1980); in the cutting edges on the trailing side the enamel is about 0.1 mm thick, of which about 30 % adjacent to the EDJ is of radial enamel, while the outer part shows distinct HSB that are thicker than those in the incisors. They are orientated transversely and in longitudinal section are slightly inclined apically.

Sciurus vulgaris L., 1758.
Recent, Southern Germany; several dentitions (KOE 32).

The enamel of the incisor is two-layered. The *portio interna* shows uniserial HSB, orientated

Source : MNHN, Paris

transversely. The HSB start at the EDJ and are generally not inclined. The *portio externa* is formed by radial enamel even if the material sometimes resists etching and therefore does not show prisms clearly. The *portio externa* occupies over 35 % of the thickness of the enamel.

Castor canadensis Kuhl, 1820 and *Castor fiber* L., 1758.
Recent, no data (KOE 91 and KOE 23).

In the incisor (*C.c.*) the enamel is two-layered. The *portio interna* shows uniserial HSB starting immediately at the EDJ. They are orientated transversely and inclined apically at about 70°. The *portio externa* is formed by radial enamel and occupies up to 55 % of the enamel thickness.

In the hypsodont cheek teeth (*C.f.*) the enamel shows thick HSB, that are transversely orientated and penetrate the entire enamel. In a longitudinal section the HSB are slightly inclined in the inner part but bend convexly towards the outer surface.

Microtia magna Freudenthal, 1976.
Upper Miocene, Gargano, (Italy); isolated molars and incisors (KOE 15, 176) (Fig. 13).

The thickness of the enamel is about 0.25 mm including the *portio externa* which occupies about 10 % of the total. The *portio interna* is formed by very regular, uniserial HSB, which are inclined at about 40°. In a very fortunate ground section (Fig. 13) the IPM can be seen to fill the gaps between the prisms, the two phases occurring over one another at about 90°. The IPM is orientated at right angles to the HSB. This internal structure of the uniserial HSB is common in incisors of myomorph rodents.

The molar enamel of this giant murid is built mainly out of the radial type. In the outer part irregularly tangential enamel is present. Between both enamel types, prisms have to turn simultaneously but remain in parallel to each other.

Cricetus cricetus (L., 1758).
Recent, Northern Germany; several dentitions (KOE 100).

The enamel of the lower incisor is about 1.3 mm thick. The *portio interna* is formed of uniserial HSB, which are inclined apically at about 40-50°. The *portio externa* occupies one third of the total thickness and is of radial enamel.

The molar crowns show only radial enamel, except for a small ring of lamellar enamel surrounding the crown at its very base (von Koenigswald, 1980).

Arvicola terrestris (L., 1758).
Upper Pleistocene and Recent, Southern Germany; several dentitions (KOE 7, 133) (Fig. 14).

An upper incisor shows an enamel of about 0.02 mm thickness. The *portio externa* with radial enamel occupies up to about 40 % of the total thickness. The HSB of the *portio interna* are inclined at 50° to the EDJ. In a tangential section the regular bifurcation of these uniserial HSB follows the same pattern as in thick HSB, for instance in *Daubentonia* (von Koenigswald & Pfretzschner, in press).

The Schmelzmuster of the molars includes uniserial HSB and radial enamel in the leading edges as well as radial enamel and tangential enamel in the trailing edges. The distribution of the various enamel types is in accordance to the stress pattern that occurs during chewing (von Koenigswald, 1980).

Ondatra zibethicus L., 1766.
Recent, Southern Germany; several dentitions (KOE 36) (Fig. 12).

The enamel, which is about 0.1 mm thick, has a *portio interna* that occupies about 80 % of the total. The uniserial HSB are inclined apically at about 40°. The *portio externa* is of radial enamel. The HSB do not start immediately at the EDJ but leave a small inner layer of radial enamel.

For a description of the complex structure of the molars see von Koenigswald (1980).

Discussion

Despite the functional similarities of enlarged anterior teeth, enamel structures vary widely. Some differences can be related to the systematic position of a taxon, but great differences may occur even within groups. Certainly, the functional adaptations are superimposed on the genetic heritage of the specific group. There is no

Source : MNHN, Paris

doubt that all enamel formation is controlled by the genome. The teeth are formed before chewing forces can act on them, and no remodeling as in bone is possible within the enamel. Even in continuously growing teeth, like rodent incisors, the enamel is formed in an area that is not exposed to chewing forces. All functional adaptations of the enamel have to be fixed in the genome, and the phenotype is the result of natural selection. That severe selection acts on enamel structures could be shown by the close correspondence of the stress pattern and Schmelzmuster in arvicolid molars (von Koenigswald, 1980, 1982).

The microstructure of the enamel in enlarged front teeth is not only determined by their specific biomechanic requirements, but also by inherited structures. Therefore the best approach would be to determine the structural change due to the biomechanical factors in enlarged teeth by a comparison of their Schmelzmuster to that of the unmodified teeth in their predecessors. This approach is only possible in very few cases, due to the incomplete fossil record. For that reason the Schmelzmuster of enlarged teeth is compared to cheek teeth of the same dentition, since it is probable that they kept an unmodified structure, unless they underwent an important morphological modification too.

Differences in the enamel structure of the cheek teeth in various groups indicate that the starting point for the further modification in enlarged front teeth was not the same for all animals.

This theoretical approach for defining the starting point must be modified when specialization of the enlarged front teeth is very old and when the molars are independently specialized. This happened, for instance, in rodents. The typical incisors were developed before their first occurrence in the early Eocene and the typical uniserial enamel in cricetids is already known in the Oligocene (Wahlert, 1968). The molars of Arvicolidae started their specialization in the Pliocene and thus give no information about the starting point of the incisor enamel. Although such cases are rare, mainly restricted to rodents, this problem has to be discussed for rhinoceroses, too.

The following discussion is arranged according to the complexity of enamel structure. To form cutting edges, a general character for enlarged front teeth, the enamel is required to be strong but not brittle. The greatest danger for a fibrous structure like enamel is cracks opened by tensile stresses that act vertically to the prism direction (Pfretzschner, this volume). Cracks tend to follow the IPM and to avoid prisms (Boyde, 1976). When all prisms are orientated straight and in parallel the danger of cracks is fairly high. To avoid cracks, prisms have to change direction or to decussate as in HSB. Such structures alter the direction of a crack or even divide the progressing crack, so that cracks lose part of their energy (Pfretzschner, this volume).

A. *Enamel with straight prisms*
(Figs. 1 and 2)

As said above, the least derived structure possible for enlarged front teeth is expected only in groups with very limited enamel differentiation. One would expect such enamel to have prisms that penetrate straight through its thickness, as in Mesozoic mammals, small marsupials, some insectivores, and bats. The prisms may rise apically but no lateral deviation is expected. This enamel type is called "radial enamel" (von Koenigswald, 1978).

The least derived stage found in enlarged incisors is present in the apatemyid *Heterohyus* (Fig. 1). The prisms, which penetrate the enamel, are almost straight and show virtually no inclination. That *Heterohyus* is so primitive is astonishing, since *Heterohyus* appears to have been as specialized as *Daubentonia*. Recently found skeletal material suggests that *Heterohyus* may have gnawed on wood to open the cavities of insect larvae (von Koenigswald, 1987b). Nevertheless, no structural differentiation protects the enamel.

A second example of enlarged frontal teeth that lack any specific differentiation is *Procavia* (Fig. 2). Stromer (1924) discussed the enamel of the molars, which are built only of radial enamel. The enamel in the incisors is very thin, but this is no argument for a missing internal structure, since rodent incisors as well as molars are well structured and have thin enamel.

The tooth size in *Procavia* and *Heterohyus europaeus* would lead one to expect a reinforcing structure (von Koenigswald, Rensberger & Pfretzschner, 1987); none, however, could be detected. *Procavia* and *Heterohyus* thus prove that quite a

Source : MNHN, Paris

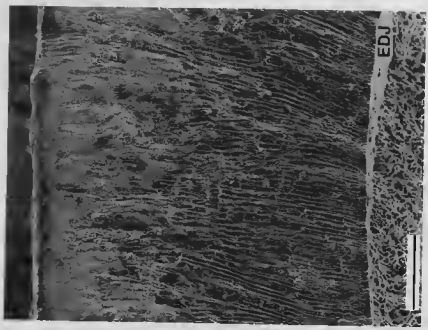

FIG. 1. — *Heterohyus europaeus*, Eocene, Egerkingen. Cross section of incisor. Despite the greatly enlarged size of the incisor, the prisms penetrate the enamel straightly. Length of bar equals 0.1 mm.

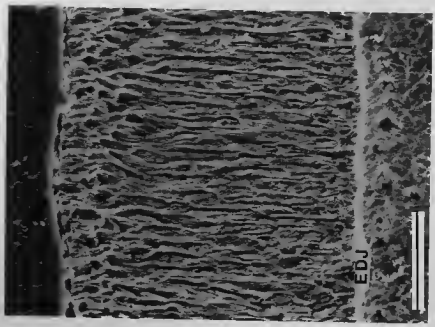

FIG. 2. — *Procavia* sp., Pleistocene, East Africa. Cross section of an upper incisor. The prisms of the very thin enamel are all in parallel and straight. Length of bar equals 40 μm.

Source : MNHN, Paris

reasonable tooth size is possible without a reinforcing structure.

The multituberculate *Taeniolabis* is a third example of straight prisms in enlarged front teeth. According to the figures of Carlson & Krause (1985) the prisms are straight but inclined apically at about 45° to the EDJ. This seems to be a slight modification compared with the very primitive enamels in *Heterohyus* and *Procavia.*

B. *Enamel with a simultaneous turn of prisms*
(Figs. 3, 4, and 5)

Compared to the straight prisms in radial enamel, a modified structure is found when prisms, still orientated in parallel, change their direction simultaneously. This happens at a specific level, which is marked in a longitudinal section as a line parallel to the EDJ; the latter is an important character for distinguishing this type of structure from the more complicated HSB. This phenomenon of a simultaneous prism turn was described for arvicolid molars as the border between the radial and the tangential enamel types (von Koenigswald, 1978, 1980). It is a widespread phenomenon and will be described as simultaneous turn of prisms. It is not a specific enamel type but the border between two types which are defined by different prism directions.

Such a simultaneous turn of prisms was found in enlarged lower and upper incisors of soricids. The border at which the prisms make their turn is parallel to the EDJ. This structure is independent of the iron stain in the outermost enamel layers. Since the molars show a very similar simultaneous turn of prisms, this structure in incisors cannot be regarded as a specific adaptation for the enlarged incisors but belongs to the general enamel structure of this group.

The enlarged lower incisors of ptilodontoid multituberculates show a two-layered enamel. According to the figures for the genera *Mesodma* (Sahni, 1979) and *Ptilodus* (Carlson & Krause, 1985) both layers differ only in the prism direction. A simultaneous turn of prisms divides the two layers. This character may differentiate the ptilodontoids from the taeniolaboids at the level of enamel structures. Since no prism turn was detected in molars, this structure can be regarded as an adaptation of the enlarged incisors.

In *Macropus rufus* and *M. giganteus* the enlarged lower incisors show a distinct simultaneous turn of prisms parallel to the EDJ (Beier, 1983, 1984). Since this feature is not found in the molar dentition, this is obviously a specific adaptation for the enlarged incisors. In addition to this very marked turn of prisms, in some kangaroos HSB also occur (Beier, 1983).

This simultaneous turn of prisms, where all prisms stay in parallel to each other and do not decussate, is not restricted to incisors. It was mentioned above that the same abrupt turn was found in arvicolid molars; it is very frequent in the molars of other myomorph rodents as well. So far only a single turn was discussed, but this turn can be doubled; after the second turn the prisms are almost in the same direction as they were before the first turn. The result is a fine strip of tangential enamel intercalated between an inner and an outer radial enamel. Such a strip of tangential enamel, caused by two turns of prisms, was found to reinforce the enamel in hypsodont molars of *Microtoscoptes*, a cricetid from the Upper Miocene (von Koenigswald, 1980, 1987a).

Such a strip of a different enamel structure is biomechanically important, since it would help to stop a crack that already has invaded the enamel. Beier (1983) figures a section through a molar of *Macropus giganteus* showing that this doubled turn of prisms may even be repeated several times. Even if Beier (1983) called them HSB this is a different structure, since the intecalated strips are much thinner than the sections of radial enamel. Prisms do not decussate but always stay parallel. Another important difference is that these intercalated strips are parallel to the EDJ, while HSB in longitudinal sections are always at an angle to the EDJ.

The sequence of a single simultaneous turn of prisms, followed by the doubled turn forming intercalated strips, and finally the repetition of this feature does not show how Hunter-Schreger bands developed. Even when the last member of the sequence shows some superficial resemblance to HSB the basic differences mark an independent origin. It must be regarded as an independent way to reinforce the enamel (von Koenigswald, 1981).

In the geological record the simultaneous turn of prisms is present already in the Lancian (Upper Cretaceous) according to Carlson &

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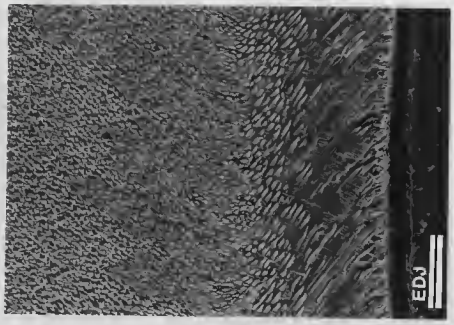

FIG. 3. — *Macropus rufus*, Recent. Cross section of a lower incisor. A single simultaneous turn of prisms is the only structure to strengthen the enamel. Length of bar equals 50 µm.

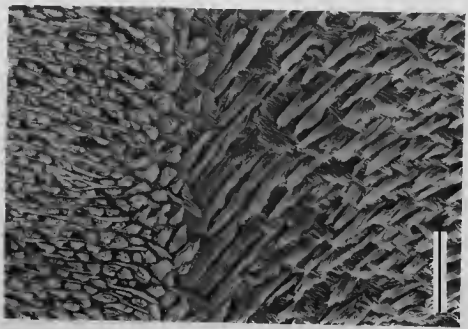

FIG. 4. — *Macropus rufus*, Recent. Cross section of a lower incisor. In a simultaneous turn of prisms all individual prisms stay in parallel and keep their neighbor. IPM forms inter-row sheets between prisms. Length of bar equals 20 µm.

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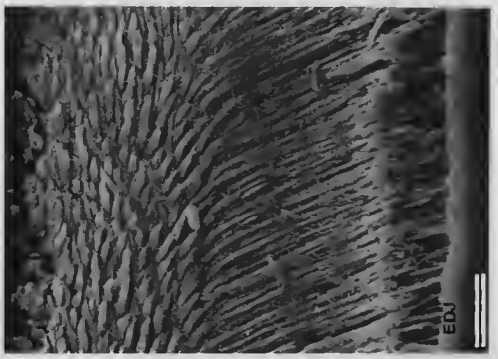

FIG. 5. — *Neomys fodiens*, Recent. Longitudinal section of an upper incisor. A simultaneous turn of prisms is found as a reinforcement in incisors as well as in molars. Length of bar equals 10 μm.

Krause (1985), while HSB were found only in the early Palaeocene (von Koenigswald, Rensberger & Pfretzschner, 1987). But obviously the simultaneous turn of prisms was invented several times in parallel according to the biomechanical requirements.

C. *Enamel with interweaving bundles of prisms* (Fig. 6)

The enamel of proboscidean molars is said to have HSB (Kawai, 1955) in the innermost layer close to the EDJ. But the decussating prisms are more likely arranged as in bundles than in bands (Boyde, 1969). The relationship to typical HSB is still unclear (Fortelius, 1985). It is possible that here an independent way to reinforce the enamel is present. But this needs further studies of fossil material.

The enamel of the incisors of *Tetralophodon* forms only a thin and narrow band. It is formed by interweaving bundles of prisms as in the innermost layer of molars. The outer layers, present in molars of *Tetralophodon*, and most other proboscideans except *Deinotherium*, are missing in the incisor enamel. The lack of these outer layers may be related to the reduced thickness of the enamel. The structure of the enamel does not show particular adaptations for the enlarged front teeth.

D. *Enamel with Hunter-Schreger bands* (Figs. 7, 8, and 9)

Hunter-Schreger bands (HSB) are layers of prisms that cross each other usually at a high angle. In longitudinal sections they are found in almost all larger mammalian teeth (Kawai, 1955). They are recognizable as light and dark bands that bifurcate regularly. An additional character that distinguishes HSB from a series of doubled prism turns is the orientation toward the EDJ. In longitudinal sections HSB are orientated rectangularly to the EDJ in an underived stage, but may be inclined or curved in derived stages. I found no example of HSB arranged parallel to

Source : MNHN, Paris

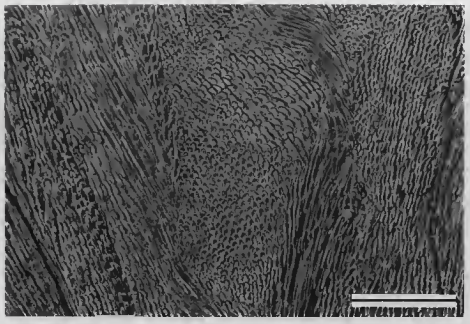

FIG. 6. — *Tetralophodon longirostris*, Upper Miocene, Eppelsheim. Cross section through the narrow band of enamel on a lower tusk. As commonly found in proboscideans, prisms are arranged in interweaving bundles. Individual prisms stick to one bundle only for a certain distance and then change to an adjacent bundle. Length of bar equals 0.1 mm.

the EDJ. The mechanical importance of HSB lies in their property to stop cracks or to divide them and deviate them into different directions, so that they lose much of their energy (Pfretzschner, this volume).

In small marsupials like *Didelphis* no HSB were found, but in larger marsupials several occurrences of true HSB have been observed (Beier, 1981, 1983, 1984). In the incisor enamel of *Petrogale* fairly thin HSB are found in the center of the lateral cutting edge, but not in the entire enamel. The restriction of HSB just to distinct areas of biomechanical importance indicates that HSB are a specific adaptation corresponding to the stress patterns of the tooth.

Vombatus and *Lasiorhinus* have well defined HSB in their continuously growing incisors. Since the rootless molars possess similar HSB it cannot be regarded as a specific enamel specialization for enlarged incisors. Because of the differences between the enamel of incisors and molars found in hypsodont rodents, the two genera discussed here seem to have developed hypsodonty and specialized enamel structure in the same evolutionary step for both the molars and incisors. But this hypothetical model should be confirmed by fossil material.

In contrast to the distinct HSB in wombats, the lack of this structure in the gigantic incisors of *Diprotodon* is very surprising. Only a very slight and irregular prism decussation could be observed, like HSB in *statu nascendi* but not comparable to the ones in wombats.

The lemur *Daubentonia* was claimed to possess a helicoidal structure that is unique among mammals (Shellis & Poole, 1979), but this cannot be confirmed here. On the contrary, HSB are developed in such a typical way that they were selected as a general model to clarify the relationship between prism course and HSB (von Koenigswald & Pfretzschner, 1987). The HSB penetrate the enamel in *Daubentonia* almost entirely and are extremely regular. In molars HSB are present, too, even though the teeth are somewhat simplified morphologically. Other lemurs like *L. catta* and most other primates show well developed HSB. Man seems to be somewhat exceptional since his enamel was thickened secondarily. The occurrence of HSB in the incisors canot be regarded as a specific adaptation. But HSB are as regular only in similar, enlarged teeth. Generally in lemurs the HSB bifurcate much more often, and this produces a more irregular picture.

Source : MNHN, Paris

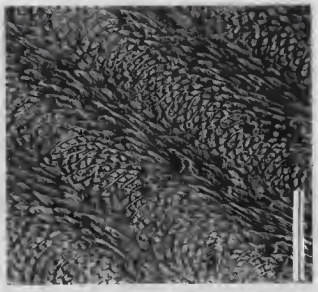

FIG. 7. — *Daubentonia madagascariensis*, Recent. Longitudinal section through lower incisor. Prisms are arranged in transverse HSB. IPM forms inter-row sheets. Length of bar equals 50 μm.

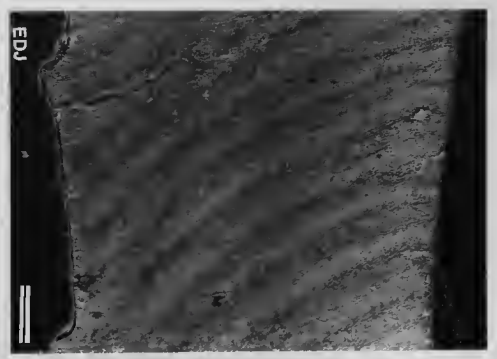

FIG. 8. — *Lama* sp.. Recent. Longitudinal section of lower incisor. Transverse HSB raise convexly from the EDJ towards the outer surface. The EDJ shows distinct transverse steps. Length of bar equals 0.1 mm.

Source : MNHN, Paris

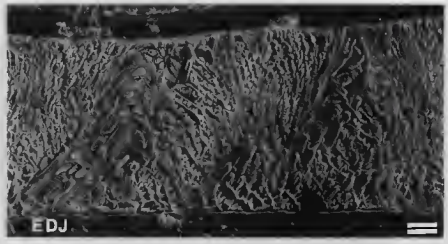

FIG. 9. — *Lepus europaeus*, Recent. Longitudinal section through a lower incisor. HSB penetrate the entire enamel. Prisms do not stick to a specific band but change from one to the next, changing its direction. Length of bar equals approximately 10 µm.

Similar conditions were found in artiodactyls, where HSB occur regularly. Of interest in terms of enlarged front teeth is the insular bovid *Myotragus* from the Pleistocene of the Baleares. The very distinct HSB are orientated tranversely, rise somewhat apically and penetrate the enamel. Hürzeler (1983) described another aberrant bovid *Maremmia* from Toscany; it has three pairs of continuously growing incisors and obviously originated from the same stock. The enamel could not be investigated but it is most probable that the front teeth show the same Schmelzmuster as in *Myotragus*.

The anterior dentition of *Maremmia* is paralleled by the South American camelids. In *Lama* the well marked HSB have the same characteristics (Fig. 8). Since the molars show HSB, only their regularity can be regarded as a specialization of the enlarged front teeth.

The huge canines of *Hippopotamus* were considered to be enlarged front teeth too, since they are only partially covered by enamel. The transverse HSB are very distinct, more so than in the molars. While HSB in sections of molars are convex, those of the canines are concave. This minor difference cannot be interpreted yet.

Among perissodactyls the hornless Rhinocerotidae developed enlarged incisors. The cheek teeth of rhinos are characterized by vertical HSB (Rensberger & von Koenigswald, 1980). Fortelius (1984, 1985) found similar vertical HSB in several other groups, too; of these only the enlarged canines of *Metamynodon* could be studied. The fact that the enamel of incisors is only one-layered while that of the molars shows two layers is regarded as a minor difference, which may be related to the thickness of the enamel.

It is highly significant that in the incisors of *Aceratherium, Indricotherium* and in the canines of *Metamynodon* the HSB are transversely orientated, while they are vertical in the molars. The vertical orientation of these HSB in the enlarged teeth corresponds with the orientation found in the other described examples. But it would be hazardous to interpret this difference between anterior dentition and cheek teeth to mean that the transverse HSB were derived from vertical ones according to different biomechanical requirements. A second possibility is that the front teeth retained transverse HSB while the enamel of the cheek teeth was rearranged into vertical HSB. Further discussion requires observation of older material with less enlarged front teeth. This was available in the taxon, *Aceratherium (Mesaceratherium) pauliacense* (Richard, 1946) from the Upper Oligocene fissure filling of Gaimersheim in Southern Germany (Heissig, 1969). The lateral lower incisors are enlarged only slightly while the mesial incisors are minute. All investigated teeth show transverse HSB. Since the incisors are not yet enlarged in this stage of evolution, the transverse arrangement of HSB cannot be a specific adaptation of these

Source : MNHN, Paris

teeth. It is more likely that a primitive character was retained here.

Besides these larger mammals the Lagomorpha and Mixodontia must be listed here too. In lagomorphs (Fig. 9) the transverse HSB penetrate the entire enamel. The undulating structure, described by Tomes (1850) and Korvenkontio (1934), occurs in any tangential section. It results from the obliqueness of the section through the prisms of different layers which have HSB structure. This picture of undulating lines can be obtained wherever HSB are sectioned in this way, e.g. in *Daubentonia* and in the hystricomorph rodents too (Fig. 11). Even in the uniserial HSB of myomorph rodents this pattern can be observed, but it is slightly modified (Fig. 14). This character does not distinguish lagomorphs from other mammals but it demonstrates that the HSB are of normal structure. While the HSB penetrate the enamel in the incisors, in molars and premolars the layer of HSB is covered by a second layer of radial enamel.

In the mixodontoid *Rhombomylus* HSB penetrate the enamel as in lagomorphs. This is not sufficient to draw systematic conclusions, since from this survey it may be deduced that well marked HSB in transverse orientation are a common solution to the biomechanical requirements of enlarged front teeth.

E. *Enamel in rodent incisors*
(Figs. 10-14)

Rodent incisors have to be discussed separately even if they have many traits in common with the teeth discussed in the previous section. The main difference in rodents is that the Schmelzmuster always kept an outer layer of radial enamel. This enamel is likely to break since the prisms are all parallel; on the other hand, the prism orientation reduces attrition (Rensberger & von Koenigswald, 1980). Rodent incisors extrude rapidly and overall attrition is of little interest; the resistance of the material on the outer side of the incisor, however, may result in an enhanced cutting edge.

HSB form at least half of the enamel thickness but often more, up to 80 %. HSB are classified according to their thickness into multiserial (more than 4 prisms), pauciserial (4-2 prisms) and uniserial (2-1 prisms) HSB. Von Koenigswald (1980, 1985) and Wahlert (1983) argue that the multiserial HSB present in so many other mammals should be the least derived status, while pauciserial and especially uniserial HSB are subsequent stages of differentiation. Pfretzschner (this volume) shows that a higher number of HSB in the same volume of enamel increases the stability.

While multiserial and pauciserial HSB are usually orientated tranversely (Korvenkontio, 1934), the uniserial HSB seem to have reached a new level of complexity, since in various groups like in eomyids (Wahlert & von Koenigswald, 1985) they are turned almost vertically.

All the specialization of enamel structure in rodent incisors happened independently from the structures in the molar dentition. While uniserial HSB are present in the incisors, *Sciurus* has multiserial HSB in its molars. In most murid molars radial enamel is dominant. In some lineages such molars became hypsodont later and new reinforcement had to be developed; that developed previously in the incisors cannot be transferred into the molars as well. The hypsodont murid *Microtia*, for instance, developed the simultaneous turn of prisms in the molars to reinforce the enamel; only a small band of uniserial HSB surrounds the tooth at the very base. The cricetid *Ruscinomys* shows the same feature (von Koenigswald, 1980). *Microtoscoptes*, mentioned above, has a layer of tangential enamel within the radial enamel of its molars that demonstrates the doubled turn of the prisms.

In arvicolids the *Mimomys* lineage first developed tangential enamel as an addition to a basal ring of uniserial HSB; thus the simultaneous turn of prisms occurs here, too. Only later in time did the uniserial HSB expand from the basal into the main cutting edges (von Koenigswald, 1980). Lemmings evolved special uniserial HSB that is specific to this group (von Koenigswald & Martin, 1984). All these specializations in the molars happen without any influence from the enamel of the incisors.

The differences between incisors and molars demonstrate that hypsodonty and enamel structure in the molars was achevied independently from these characters in the incisors. This is obvious from the known fossil record of rodents, but may be used also to interpret the conditions in wombats.

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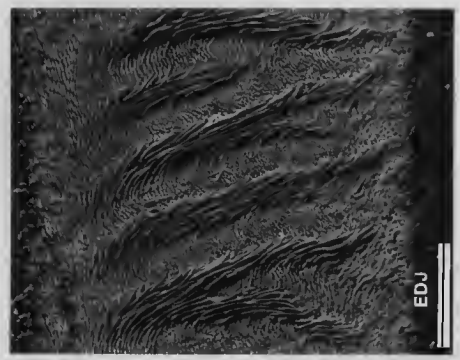

FIG. 10. — *Chinchilla laniger*, Recent. Longitudinal section through an incisor. Multiserial HSB bifurcate frequently and leave a distinct outer layer of radial enamel (*portio externa*). Length of bar equals 0.1 mm.

FIG. 11. — *Chinchilla laniger*, Recent. Tangential section through the *portio interna* of a lower incisor. HSB show bifurcations as in the plane of the section, too. The different inclination of the prisms belonging to different HSB causes an undulating lineament similar to the one described as "typical" for lagomorphs. Length of bar equals 40 µm.

Source : MNHN, Paris

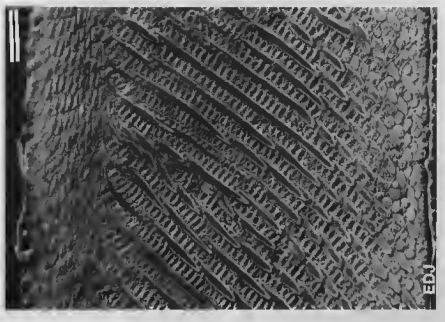

FIG. 12. — *Ondatra zibethicus*, Recent. Longitudinal section of a lower incisor. The *portio interna* with uniserial HSB forms about 80 % of the entire enamel. Prisms decussate at about 90°. The IPM penetrates the bands at about 90°, too. Length of bar equals 20 μm.

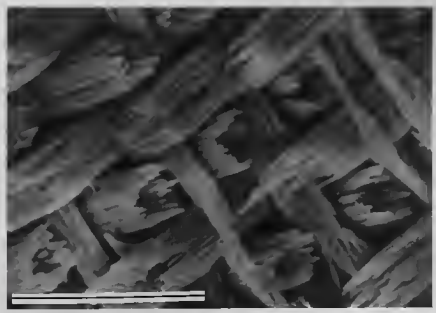

FIG. 13. — *Microtia magna*, Upper Miocene, Monte Gargano. Oblique section through the *portio interna* of a lower incisor. All three directions are strengthened by fibers, two by prisms of different HSB, the third by the IPM (diagonal from the left to the right). Length of bar equals 10 μm.

Source : MNHN, Paris

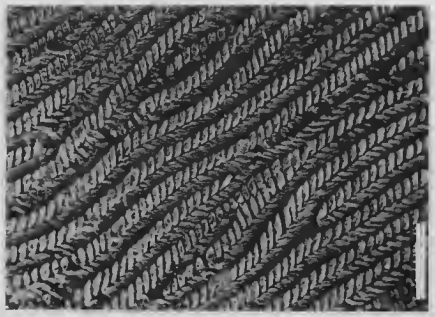

FIG. 14. — *Arvicola terrestris*, Recent. Tangential sections through the *portio interna* of the lower incisor. The uniserial HSB bifurcate in a normal pattern and the undulating lineament of multiserial HSB (as in Fig. 11) is reduced to a zig-zag pattern of the individual prisms. Length of bar equals 20 μm.

CONCLUSION

The survey of the enamel structures in enlarged front teeth among mammals does not offer a homogeneous picture. Differences are due to the fact that enlarged front teeth were developed independently many times. Nevertheless, the number of possible structures in the enamel is limited. Only four major Schmelzmuster were met.

a. The most primitive enamel with a straight prism course throughout the enamel was found only as an exception for three groups (taeniolaboid Multituberculata, Apatemyidae, and Hyracoidea). This enamel is highly likely to be destroyed by cracks, but it may be more resistant to wear, since the prisms are strongly inclined to the EDJ. This primitive enamel is mainly associated with small body size but was found in Hyracoidea, too, which include some quite large fossil forms.

b. A simultaneous turn of prisms within the enamel with the trait that all prisms stay in parallel to each other gives some reinforcement, since cracks are at least deviated or even stopped at this turn. This Schmelzmuster was found in the enlarged front teeth of the ptilodontoid Multituberculata, Soricidae and several Marsupiala.

The pattern of occurrence among mammals shows that this structure was developed several times in parallel. It forms a structure basically different from decussating prisms in HSB.

c. Hunter-Schreger bands are a common structure of the enamel among mammals and they certainly developed several times in parallel. They were found in enlarged front teeth in some Marsupialia, most Primates, Artiodactyla, Perissodactyla, Notoungulata, Lagomorpha, and with bands of reduced thickness in rodents. The decussating prisms are a structure that prevents crack propagation, especially when the bands are fairly thin.

d. Interweaving bundles of prisms are found in the innermost layer of cheek teeth in proboscideans. Whether they developed from HSB or whether they are an independent structure that reinforces the enamel is still in question. This structure was found in the narrow enamel band of the tusk of *Tetralophodon*.

Source : MNHN, Paris

A regular arrangement of prisms in layers, like HSB, requires less genetic information for the movement of ameloblasts than does the free interweaving of prism bundles in three dimensions as in this type of enamel. The biomechanical value of interweaving prism bundles may even be higher than that of HSB, since bands open at least one plane from which cracks may invade the enamel. But the orientation of these layers may be parallel to tension forces so that the probability of cracks in this plane is reduced.

An interweaving of single prisms, as in the enamel of molars of the Lemminae and several other rodent groups, was not found in the enlarged front teeth.

The Schmelzmuster in the enlarged front teeth were found in cheek teeth as well, so these structures indicate a possible way to reinforce the enamel.

In the dentition of a single individual the enamel of enlarged front teeth may differ markedly from those of underived cheek teeth and represent specialization in accord with biomechanical requirements.

Straight prisms, the least derived condition, do not constitute a specific adaptation. It is possible that in some groups the ability to modify enamel structure is blocked.

The simultaneous turn of prisms in the enamel of enlarged front teeth can be regarded as a specific adaptation, where this structure is not present in the cheek teeth. This case occurs in ptilodontoid Multituberculata and in some of the larger Marsupialia. In soricids this structure is present in molars, too, and the morphologically derived front teeth do not show any additional modification of the enamel.

HSB may be regarded as a specific adaptation in enlarged front teeth in only some members of the Marsupialia and in the Rodentia generally. The majority of enlarged teeth that show HSB belong to the Primates, Artiodactyla, Perissodactyla, Notoungulata and Lagomorpha, where HSB are present in the rest of the dentition as well.

Nevertheless, some general features of enlarged front teeth may distinguish them from the molar dentition. First, the enamel is always thin in the enlarged teeth. When the enamel of the cheek teeth is two-layered, possessing a thick layer of radial enamel on the outside, the enamel of the enlarged front teeth corresponds only to the inner layer with HSB, as in Rhinocerotoidea or Lagomorpha. In Artiodactyla the HSB of enlarged front teeth tend to be more distinct than in the cheek teeth and to penetrate the entire enamel thickness. Only minor layers of outer or inner radial enamel may be left. Generally the HSB of the enlarged front teeth are very clearly marked and orientated transversely, even if they are orientated vertically in the molars of the same dentition; this condition was found in some Rhinocerotidae as well as in Amynodontinae. Astrapotheria form a third example. Even when the biomechanical stress pattern may be highly variable in the different enlarged front teeth, the transverse orientation of multiserial HSB may be optimal.

The enamel of the cheek teeth in the Carnivora regularly shows HSB as do the enlarged canines. Since the orientation for these HSB is transverse too, this group, not studied in particular here, fits into the general scheme.

In rodents the HSB are usually orientated transversely too. When the HSB are thinned out to uniserial bands, they reach an almost isotropic structure with reinforcement by prisms and IPM in three different directions. In some rodents with such uniserial HSB tranverse orientation is abandoned and HSB may be rearranged almost vertically. Rodent incisors characteristically retain an outer radial enamel (*portio externa*). It is not yet possible to determine the factors that control the thickness of this layer.

Normally the enlarged front teeth may be regarded as more specialized than the cheek teeth. Therefore, the HSB in rodent incisors were regarded as a specific adaptation. But in many rodents an independent differentiation of the molars happens, affecting tooth morphology as well as enamel structure. Thus a great variety of enamel structures is found in the molar dentition, especially when the molars become evergrowing. A well studied example is the arvicolids in which the Schmelzmuster is much more complex than in the incisors. This shows that the differentiation of the molars occurred independently after the specialization of the incisors. Another example that documents this independent development of the molars was found in the Rhinocerotidae, in which the HSB turned vertically, while they remained transverse in incisors.

Source : MNHN, Paris

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Source : MNHN, Paris

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Caractérisation et Datation d'Émail Dentaire de Vertébrés Fossiles par des Méthodes Radionucléaires

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ABSTRACT

Both fossil marine and continental vertebrate dental enamel have been studied by different physical methods: Electron Spin Resonance (ESR) spectrometry, γ-spectrometry and analytical measurements:

Continental vertebrates: *Elephas, Cuvieronius* (High Andes mastodonte), *Hippopotamus, Rhinoceros, Bos, Equus, Cervus*, display practically the same ESR pattern due to the electronic centers created first in the hydroxyapatite and carbon-apatite mineral phase mainly by uranium-series radiations, second from the proteinic phase following reactions between radicals produced by radiations — methylation of the alanine amino-acid is one of the processes —. The intensity of some ESR lines is proportional first to the amount of uranium trapped in apatites and second to the irradiation time elapsed since fossilization, leading to the age of the fossil. Presently, ESR dating of fossil enamel can be obtained from about 200.000 years to 3 millions years. Extension to the Würm period and to the Miocene is in progress.

Marine vertebrates: *Delphinidae, Isuridae* display a similar ESR but a more complex pattern requiring more study before dating.

Briefly, such physico-chemical characterization has already led to valuable paleontological data on the

RÉSUMÉ

L'émail dentaire de vertébrés fossiles continentaux et marins a été étudié par différentes méthodes physiques : Résonance Paramagnétique Electronique (RPE), Spectrométrie-γ et autres méthodes analytiques (spectrométrie de masse), avec les résultats suivants :

Mammifères continentaux : l'émail dentaire des genres *Elephas, Cuvieronius* (mastodonte des Andes) *Hippopotamus, Rhinoceros, Bos, Equus, Cervus*, présente un spectre RPE typique dû aux centres électroniques créés *post mortem* d'une part dans l'hydroxy- et la carbonate-apatite, principalement sous l'effet des radiations émises par l'uranium et ses descendants radioactifs et d'autre part à la suite de réactions entre radicaux engendrés par irradiation — la méthylation de l'alanine étant l'un des processus possibles —. L'intensité de certaines raies du spectre RPE est proportionnelle à la fois à la teneur en uranium piégé dans les apatites et au temps écoulé depuis la fossilisation. Leur mesure constitue donc un moyen de datation. Actuellement le domaine de cette méthode chronométrique s'étend entre environ 200 000 ans et 3 millions d'années. Des travaux en cours sur des échantillons plus récents (Würm) et plus anciens (Miocène) devraient permettre de fixer ses limites pratiques d'application.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 169-176.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

mineralization-fossilization process, on the aging processes and finally on the age of continental vertebrates in the Plio-Quaternary period.

According to the fission-track method applied on a *Cervus* tooth 2.5 Ma old:

— uranium amount in dentine is high (325 ppm), more than 10 times higher than in enamel.
— uranium is evenly distributed in dentine, but is lying in a thin damaged surface-layer (about 0.1 mm thick) of enamel.
— uranium in dentine seems to originate from natural waters through the root, but is penetrating into the enamel when some chemical degradation process happens.

Introduction

Les dents des vertébrés fossiles présentent un grand intérêt en paléontologie à deux égards. D'une part parce qu'elles sont souvent de bons marqueurs de la spéciation des lignées évolutives, d'autre part parce que ce sont les parties du squelette parmi les plus résistantes á l'action dissolutive des eaux de circulation superficielles. Ce sont donc des restes fossiles qu'il est particuliérement important de caractériser et de dater le plus précisément possible, notamment si l'on veut mesurer la vitesse d'évolution d'un phyllum. Jusqu'á récemment, ces datations, hormis du Pléistocéne Supérieur á l'Actuel (avec le Carbone-14 pour les quarante derniers milliers d'années, ou les méthodes de datation par le déséquilibre des séries radioactives de l'Uranium pour les derniers 350 000 ans) étaient toujours indirectes (magnétostratigraphie, datations de niveaux volcaniques stratigraphiquement proches ou associés aux restes fossiles, ,,,).

En 1978, Ikeya suggéra que les ossements et dents de vertébrés fossiles pourraient être datés par des mesures de Résonance Paramagnétique Électronique (RPE) [1]. Cette idée a été reprise dans différents laboratoires, dont, dès 1981, par le Groupe de Géochronologie et de Géochimie Isotopique de l'Université de Grenoble 1 qui a proposé (Bouchez, 1981 ; Ma, 1984) une méthode originale de datation des dents fossiles Plio-Quaternaires par la mesure RPE de leur émail. Au cours de ces travaux, il est apparu que la RPE se montrait capable, par ailleurs, de permettre une certaine caractérisation de l'état physico-chimique de cet émail. Nous présentons ci-dessous l'état de nos connaissances actuelles en ce domaine.

1 en anglais, Electron Spin Resonance (ESR).

Vertébrés marins : l'émail de *Delphinidae* et d'*Isuridae*, posséde un spectre RPE analogue, mais plus complexe que celui des vertébrés continentaux. Dans l'état actuel des travaux il n'est pas encore envisageable de l'utiliser en datation.

La RPE et les techniques qui lui sont associées pour la datation de l'émail dentaire fossile peuvent donc conduire á une meilleure connaissance des processus de fossilisation des tissus dentaires et de l'évolution de leur structure physico-chimique *post mortem*. Elle paraît pouvoir constituer une méthode de chronométrie de l'émail dentaire pour la période plio-quaternaire. Sa limite inférieure d'application vers le Miocéne n'est pas encore établie.

Méthodologie

Toute dent est constituée de trois tissus fondamentaux : émail, dentine et cément. Chez les vertébrés continentaux fossiles seul l'émail peut présenter (pour les fossiles suffisamment anciens) un spectre RPE utilisable et composé de raies d'absorption relativement étroites et parfois trés intenses par rapport au bruit de fond (Fig. 1). Une autre propriété remarquable de l'émail est que ces raies sont susceptibles d'une augmentation significative de leur intensité sous l'effet d'une exposition à un flux de particules ionisantes.

Une des propriétés notables des apatites d'une couche d'émail dentaire est que les cristaux qui la constituent présentent tous sensiblement la même orientation, leurs axes cristallographiques c étant parallèles à sub-parallèles entre eux á une échelle sub-millimétrique á millimétrique. Une conséquence importante de cet arrangement géométrique est qu'il permet aisément une étude de la symétrie spatiale des centres électroniques responsables des transitions observées dans le spectre RPE et par lá même, de préciser la nature de ces centres.

Les spectres discutés ci-dessous ont donc été pris sur des fragments d'émail dentaire de 2 mg à 50 mg, orientés dans la cavité de résonance du spectrométre RPE par rapport á la direction du

Source : MNHN, Paris

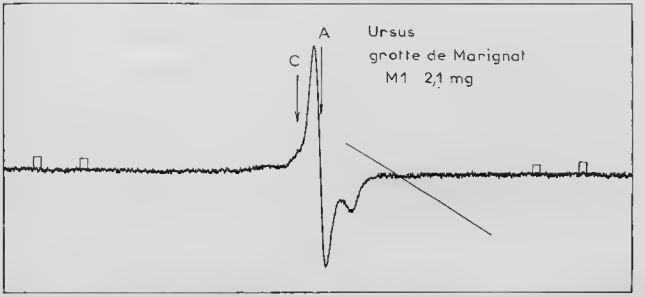

FIG. 1. — Spectre RPE d'un fragment d'émail d'une molaire de *Ursus denengheri* provenant de la grotte de Marignat (Vercors), étudiée par le Dr. Caillat. Les marques sur la ligne de base du spectre sont celles faites pour le calcul automatique de l'intensité du signal. L'échelle des abscisses du champ magnétique B est la même pour les Figs. 1 à 4 ; elle est indiquée sur la Fig. 5.

champ magnétique statique $\vec{B}$; un spectromètre Varian opérant dans la bande X a été utilisé avec un champ statique B ~ 3 300 Gauss et une modulation de 100 kHz et de 0,5 Gauss d'intensité ; la puissance était limitée à ~ 0,1 mW afin d'éviter les effets de saturation du signal.

Ces spectres ont été pris sur l'émail dentaire de vertébrés fossiles continentaux (Figs. 1 à 3) et marins (Fig. 4). Ils comportent tous deux transitions principales répérées par les lettres A et C, et presque tous (Figs. 2 à 4) un septet de raies d'intensité très inférieure à celle de l'ensemble A-C. Il apparaît aussi que les spectres de l'émail des vertébrés marins sont marqués par une plus grande complexité que ceux de leurs congénères continentaux.

RÉSULTATS

A. *Spectres RPE d'émail de vertébrés continentaux*

Le spectre le plus simple est celui de *Ursus* provenant d'un niveau du Pléistocène Supérieur de la Grotte de Marignat (Vercors). Ce spectre (Fig. 1) comporte principalement la transition A, correspondant à un centre électronique, fortement anisotrope, et à symétrie axiale autour de l'axe cristallographique ĉ comme le sont les autres centres discutés dans cet article. Il est caractérisé par un facteur spectroscopique dont les composantes, parallèle et perpendiculaire, sont respectivement égales à : $g_{\perp} \sim 2{,}0018$ et $g_{//}$ 1,9977 ($\vec{c} \perp \vec{B}$, Fig. 4, et $\vec{c}//\vec{B}$, Fig. 3). On considère qu'il pourrrait s'agir d'un centre électronique Q porté par l'axe c ; ce centre n'est détruit qu'au-dessus de 400° C ; on peut donc le considérer comme stable géologiquement dans les restes dentaires fossiles au cours du Plio-Quaternaire.

La transition C est bien développée après un recuit isotherme de l'émail à 300° C (Fig. 3) ; elle est isotrope et son facteur g ~ 2,0056 est égal à celui mesuré pour la raie d'absorption par exemple par Yokoyama *et al.*, (1981) et Poupeau *et al.*, (1984) dans la calcite de nombreux spéléothems. Cette transition C est due vraisemblablement à un centre électronique d'un radical carboxylique provenant de la carbonate-apatite de l'émail ; la phase carbonate-apatite en effet est manifestement présente (Doi, 1979) dans l'émail dentaire d'un vertébré avant toute fossilisation. L'augmentation de son intensité sous irradiation

Source : MNHN, Paris

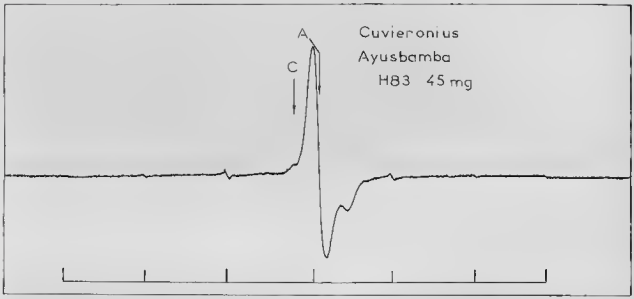

FIG. 2. — Spectre RPE d'un fragment d'émail d'une molaire de *Cuvieronius hyodon* (un mastodonte des Andes Centrales), d'âge environ 1,1 MA, provenant du site d'Ayusbamba au Pérou, étudié par le Dr. J. A. Ramirez-Pareja à Cuzco. Au-dessous du spectre sont indiquées les positions des raies du septet dû à un radical libre di-méthyle.

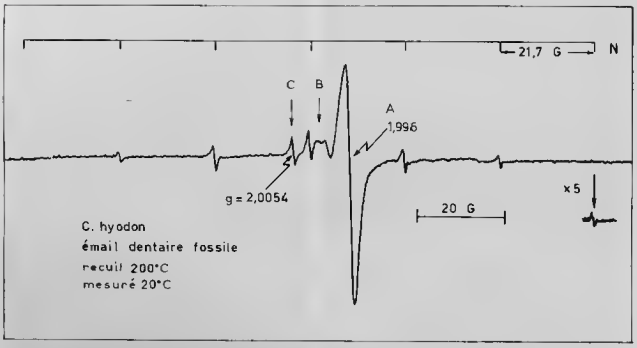

FIG. 3. — Spectre RPE, analogue à celui de la Fig. 2, obtenu avec les fibres d'émail parallèles à la direction du vecteur magnétique B. Les positions du septet diméthyle sont indiquées au-dessus du spectre. Les valeurs précises du facteur g sont (2,0056 ± 0,0001) pour la raie C et g = 1,9977 ± 0,0001 pour la raie A.

Source : MNHN, Paris

peut constituer un marqueur de l'âge fossile, si toutefois la carbonatation *post mortem* de la phase d'hydroxylapatite de l'émail contribue peu à la transition C.

Le spectre RPE de l'émail dentaire de vertébrés fossiles peut aussi comporter un troisième élément sous forme d'un septet hyperfin isotrope et d'espacement inter-raies de ~ 22 Gauss ; ces raies s'affinent avec la température puis disparaissent, d'une façon irréversible, avec la destruction du centre électronique vers 280° C. Un tel comportement est typique d'un radical organique libre de tourner dans une cavité. Ikeya (1981) avait d'abord observé un quintet et l'avait attribué au radical Alanine, mais une étude plus détaillée de ce centre par notre groupe (Bouchez *et al.*, 1987) conduit à l'attribuer à un radical diméthyle ; cette molécule n'étant pas produite naturellement, sa présence dans l'émail dentaire correspondrait à une méthylation de l'acide aminé alanine à la suite de l'irradiation de ce tissu dentaire par la radioactivité naturelle. En raison de sa plus faible stabilité thermique et de son origine complexe, ce centre ne paraît pas susceptible d'utilisation en datation, mais il constitue une caractérisation physico-chimique précieuse de la phase d'origine organique de l'émail dentaire fossile.

Une dernière transition, notée B, qui apparaît sur la figure 3 entre la transition A et la raie centrale du septet hyperfin, correspond à un centre électronique de stabilité encore plus faible, son intensité diminuant dès 200° C en même temps que celle de la raie C augmente.

Le spectre RPE de l'émail de dents fossiles de vertébrés continentaux actuels ne présente aucune des structures décrites ci-dessus. Transitions A, B et C, septet hyperfin sont donc des structures acquises *post mortem*. De ces structures, seule la transition A semble correspondre à un centre électronique suffisamment stable thermiquement pour qu'une utilisation en géochronologie soit envisageable. Ces structures ont été jusqu'à présent relevées dans les dents des genres suivants : *Cuvieronius* (mastodonte), *Elephas, Hippopotamus, Equus, Bos, Cervus* et *Ursus*. Il semble donc que ces transitions doivent présenter un certain caractère de généralité chez les vertébrés continentaux.

B. *Spectres RPE d'émail de vertébrés marins*

Le spectre de la Fig. 4 présente les mêmes caractéristiques générales que celles des vertébrés continentaux. Il s'agit de celui de la lame d'émail superficielle qui coiffe les dents de *Carcharodon carcharias* provenant du site de Sacaco, Pérou ; il comporte à la fois les transitions A, B et C et le septet organique hyperfin de méthylation de l'alanine. Toutefois, les intensités relatives de ces raies d'absorption et leur forme même peuvent différer quelque peu de celles des vertébrés continentaux. Ainsi la transition C du carbonate de même que le septet hyperfin apparaissent plus développés ; la transition B apparaît plus développée et se révèle d'interprétation plus délicate que pour les vertébrés continentaux.

L'utilisation de la transition A — qui constitue le signal principal de datation RPE pour les vertébrés continentaux en géochronologie — exige pour les vertébrés marins une étude préalable (en cours) de la structure fine de leur spectre RPE.

C. *Datation par RPE de l'émail dentaire des vertébrés continentaux*

L'utilisation de la RPE pour la datation de l'émail dentaire des vertébrés continentaux repose sur les hypothèses suivantes :

1. La transition A est d'origine purement radiogénique. Elle est nulle pour tout vertébré vivant. Après la mort d'un individu, sa croissance est uniquement due aux flux de particules ionisantes qui traversent l'émail (radioactivité naturelle, rayonnement cosmique).

2. Les centres électroniques ainsi créés sous irradiation sont suffisamment stables pour permettre de dater un spécimen du Quaternaire au Pliocène.

3. Étant donné que dans un émail de 1 million d'années, exposé à une dose annuelle de 1 rad, la création de centres électroniques correspond à une concentration de 5.10^{-4} environ, les phénomènes de saturation ne semblent pas pouvoir limiter dans le temps leur production, tout au moins pour la période Plio-Quaternaire.

4. La teneur actuelle en Uranium, Thorium et Potassium de l'émail dentaire fossile a été acquise

Source : MNHN, Paris

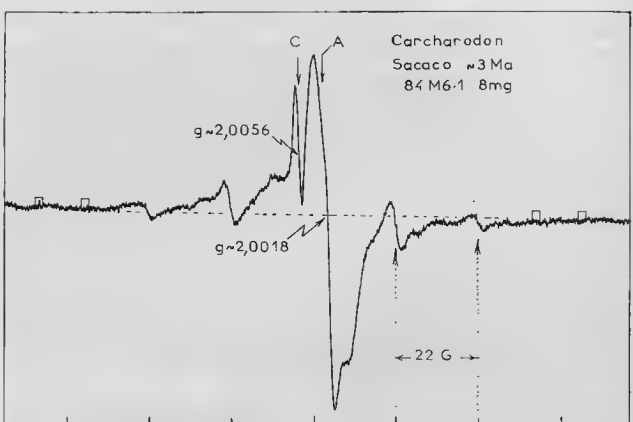

FIG. 4. — Spectre RPE d'un fragment d'émail dentaire de *Carcharodon carcharias*, d'âge environ 3 MA, provenant du site de Sacaco au Pérou, étudié par le Dr. C. de Muizon.

post mortem en un laps de temps court comparé à l'âge du fossile : la teneur en Uranium d'une dent fossile est couramment 10^4 à 10^5 fois plus forte que chez un individu vivant. Après la mort, l'Uranium se fixe essentiellement dans la dentine et le cément.

5. Après une courte période de minéralisation-fossilisation et jusqu'à l'actuel, les seules modifications de la teneur en radioéléments d'une dent fossile et de son environnement sédimentaire immédiat (dans une sphère de rayon ~ 30 cm) sont dues à la décroissance radioactive (système « clos » pour la migration des radioéléments).

Dans ces conditions, l'intensité spécifique C (nombre de spin/g) de la transition A doit croître linéairement avec le temps t selon (Bouchez *et al.*, 1984) :

$$C = R.d\ .t \quad (1)$$

où d est la dose annuelle d'irradiation délivrée dans l'émail. On la calcule à partir des teneurs mesurées en Uranium, Thorium et Potassium dans l'émail et la dentine au contact ainsi que dans les matériaux (sédiments, ossements, ...) situés dans leur environnement immédiat.

Les données obtenues dans différents laboratoires semblent indiquer que pour les quelques derniers millions d'années, les hypothèses 1 à 3 sont raisonnables. Il est beaucoup plus difficile de supposer que les hypothèses 4 et 5 soient toujours respectées. Les premiers résultats obtenus à Grenoble semblent indiquer qu'elles ne seraient en fait pas excessives, du moins pour les dents de cinq sites d'âge plus ou moins précisément connu pour lesquelles nous avons déterminé les paramètres C et d de l'équation (1).

Il apparaît en effet que la valeur du rapport C/d croît quasilinéairement pour ces cinq séries

Source : MNHN, Paris

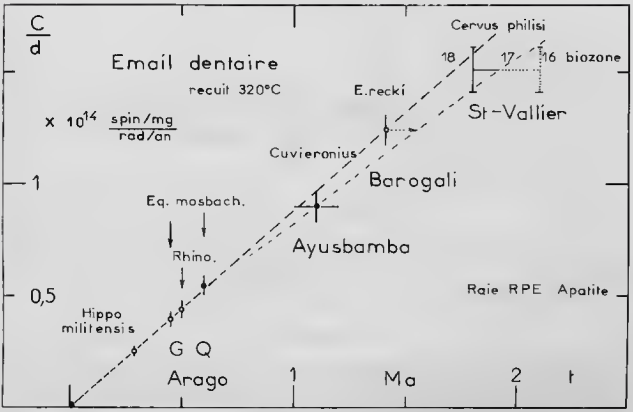

FIG. 5. — Courbe chronologique expérimentale, passant par l'origine, permettant d'obtenir l'âge RPE d'un vertébré continental à partir de la densité, par unité de dose annuelle d'irradiation, des centres électroniques de son émail dentaire.

d'échantillons comme prévu par (1). La courbe ainsi définie peut donc être utilisée comme courbe de calibration pour la détermination graphique de l'âge RPE d'un échantillon dentaire d'âge inconnu, à partir de la mesure de son rapport C/d.

Nous considérons que la courbe de la Fig. 5 a valeur de courbe de calibration provisoire pour la détermination de l'âge apparent des dents fossiles en raison du petit nombre de points sur lesquels elle est construite. Nous travaillons en ce moment à l'élargissement de ce nombre de points à la fois dans le domaine d'âge déjà couvert par cette courbe mais aussi à son extension temporelle jusque vers cinq millions d'années et au-delà afin de déterminer la limite d'application de cette méthode. Telle quelle est, cette courbe provisoire de calibration semble permettre des datations entre ~ 200 000 ans et deux millions d'années avec une précision d'environ 15 %.

CONCLUSION

La fossilisation des dents de vertébrés continentaux comprend au moins deux processus : la minéralisation de l'émail et de la dentine d'une part, et d'autre part la dégradation, sous irradiation naturelle, des apatites et des protéines qui ont servi à leur formation.

L'utilisation de méthodes physiques telles que la spectrométrie de résonance paramagnétique électronique (RPE), la spectrométrie des rayons X et γ, l'activation neutronique, la dilution isotopique de l'Uranium avec spectrométrie de masse, associées aux méthodes classiques d'analyse, permet l'étude de ces processus de fossilisation, et parfois de déterminer l'âge du fossile :

— Outre des éléments stables (Fe, Mn, Si, Al, ...) fixés surtout dans la dentine, les lanthanides y sont observés par dizaines de ppm.

Source : MNHN, Paris

— Les radioéléments naturels, essentiellement l'uranium, sont détectés surtout dans la dentine, parfois par centaines de ppm, alors que le thorium y est peu abondant, de l'ordre de 1/10 de ppm, ainsi que le potassium, de l'ordre de 0,01 % ; dans l'émail, il n'y a pratiquement pas de thorium ni de potassium, seulement de l'uranium en surface, de l'ordre du ppm dans 1/10 mm d'épaisseur, souvent dans la partie blanchie par la biodégradation des organismes.

— La dégradation de la phase d'hydroxylapatite de l'émail est observée par l'intermédiaire des centres électroniques produits par l'ionisation des rayonnements X et γ et des particules (α et électrons) naturels ; progressive jusqu'à vers 2 millions d'années, elle semble s'accélérer par la suite (elle est en cours d'étude au-delà de cinq millions d'années).

— La dégradation de la phase organique de l'émail est plus complexe. Il est bien connu que les acides aminés se racémisent, l'alanine en est un exemple. De nouveaux processus de dégradation sont observés : par exemple, la méthylation. Des radicaux de di-méthyle sont abondants, au moins jusqu'à 2 MA ; par la suite, vers 5 MA, ils semblent disparaître. Au-delà, de nouveaux processus de dégradation interviennent certainement ; il est connu que de simples radicaux de méthyle sont observés dans des silex mésozoïques.

— L'âge d'un fossile — proboscidés, équidés, bovidés, cervidés ... — peut être déterminé (à environ 15 %) à partir de la densité des centres électroniques produits par unité de dose annuelle des radiations ionisantes, jusqu'à 2 millions d'années. Des fossiles, entre 2 et 5 millions d'années, sont en cours de datation avec un espoir raisonnable.

Remerciements

Cette étude physico-chimique sur l'émail dentaire de vertébrés fossiles est conduite par le Groupe de Géochronologie et de Géochimie Isotopique de Grenoble I en collaboration avec les paléontologistes Claude Guérin (Institut de Géologie de Lyon I) pour les vertébrés continentaux et Christian de Muizon (Muséum national d'Histoire naturelle de Paris) pour les vertébrés marins, ainsi qu'avec M. Condomines de l'Institut de Géologie de l'Université de Clermont-Ferrand pour la méthode de dilution isotopique de l'uranium.

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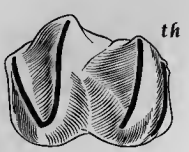
Source : MNHN, Paris

DENTAL MORPHOLOGY AND EVOLUTION



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The Dentition of Palaeozoic Lungfishes: a Consideration of the Significance of Teeth, Denticles and Tooth Plates for Dipnoan Phylogeny

M. M. SMITH

ABSTRACT

A critical review of the literature revealed that many descriptive terms for the dentition of lungfishes are used ambiguously and are frequently too imprecise to allow relationships amongst dipnoans to be accurately assessed from the dental characters. It was also apparent that there is no accepted view of the primitive condition for the dentition of dipnoans.

A model for the primitive gnathostome condition, in which there are both oral denticles and teeth, as proposed by Reif (1982), is applied to dipnoan dentitions and attempts are made to distinguish denticles from teeth in all fossil genera with suitable preservation of morphology. The proposition is, that the locus of formation of dental structures can be predicted from fossil specimens and that the distinction between denticles and teeth can be made, and is a useful one for the purpose of deciding on relationships. As a result, it is proposed that two different developmental and morphological types of dental plates can be distinguished: 1) *dentine plates*, where the development and growth is entirely from superficial denticles added at the margins, with no teeth forming; 2) *tooth plates*, in which both teeth arranged in radial rows, and denticles formed at the margins, contribute to the structure.

Recent observations on four genera, important to this discussion, are presented and their dentitions assessed from the basis of the presence or absence of denticles and teeth. From this, a scheme for reclassification of dipnoans with dental plates is proposed in

RÉSUMÉ

Un examen critique de la littérature scientifique révèle que nombre de termes descriptifs employés pour la denture des Dipneustes sont utilisés de façon ambiguë et sont fréquemment trop vagues pour permettre l'établissement de relations précises entre les Dipneustes d'après les caractères dentaires. Il est également apparu qu'il n'y a pas de consensus sur l'état primitif de la denture chez les Dipneustes.

L'auteur applique aux Dipneustes un modèle de la condition gnathostome primitive, dans laquelle il existe à la fois des denticules et des dents, comme proposé par Reif (1982), et tente de distinguer les denticules des dents de tous les genres fossiles chez qui la morphologie est préservée de façon convenable. Il est proposé que le lieu de formation des structures dentaires peut être prédit à partir des fossiles et que la distinction entre denticules et dents peut être faite, et qu'elle est utile dans l'établissement des relations de parenté. En conséquence l'auteur propose de distinguer deux types de plaques dentaires différentes par leur morphologie et leur développement : 1) *les plaques de dentine* où le développement et la croissance se font entièrement par l'adjonction de denticules superficiels sur les bords, sans formation de dents ; 2) *les plaques dentaires* auxquelles contribuent à la fois les dents disposées en rangées radiaires et les denticules formés sur les bords.

Des observations récentes sur quatre genres, importants dans cette discussion, sont présentées, et leur dentition établie, sur la base de la présence ou

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986. Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 179-194.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

which a recently described genus, *Speonesydrion iani* Campbell & Barwick, is considered to be the morphotype of the primitive condition for those with tooth plates, and also probably for those with dentine plates. The possibility of *Holodipterus gogoensis* Miles having retained elements of the primitive condition for all dipnoans is discussed.

l'absence de denticules et de dents. A partir de cela, l'auteur propose un schéma pour une nouvelle classification des Dipneustes pourvus de plaques dentaires, dans laquelle le genre récemment décrit *Speonesydrion iani* Campbell et Barwick est considéré comme le morphotype de la condition primitive pour ceux qui ont des plaques dentaires et probablement aussi pour ceux pourvus de plaques de dentine. La possibilité que *Holodipterus gogoensis* Miles ait conservé des éléments de la condition primitive à tous les Dipneustes est discutée.

Introduction

One of the two distinctive characteristics of lungfishes selected by White (1966) is the dental system; paired, fan-shaped dental plates developed on the pterygoids and prearticulars. These, together with a small gape and powerful bite, are an essential part of the adaptations for crushing food considered to distinguish the Dipnoi from crossopterygians early in their evolutionary history. Other characters associated with this mode of feeding are the reduction or loss of marginal jaw bones and marginal teeth.

The assumption that paired radiate dental plates are primitive for all dipnoans is, however, contentious. As Denison (1974, p. 31) pointed out, in dipnoans of the Devonian period at least one third of the genera did not possess tooth plates, and the chronological occurrence of early lungfishes without tooth plates led him to reject the idea that those with ridged tooth plates gave rise to all those without. Also, it is immediately obvious from the literature that it has not been possible to use the terms dental plate and tooth plate with any precision (Denison, 1974, p. 32). It is one of the objectives of this paper to clarify usage of these terms.

In a review on the evolution of the Dipnoi, Westoll (1949) had recognised that the triturating dental plates were an early adaptation, probably prior to changes in body form and fins, and had assumed that the primitive condition would be the possession of well developed conical teeth as well as a shagreen of denticles. Whereas the recognition of conical teeth has been contentious, scattered denticles have been described in several early and late genera. However, the relevance of teeth and denticles to the evolution of tooth plates has been much debated (Westoll, 1949, p. 167; White, 1966, p. 7; Denison, 1974, p. 53; Miles, 1977, p. 296; Campbell & Barwick, 1983, p. 17, 1984, p. 45, 1985, p. 314, 1986). There is at present little agreement on which of the early genera possess tooth plates and which is the primitive condition, with tooth plates or without; or on whether or not tooth-plated dipnoans are a monophyletic group as proposed by Miles (1977, p. 299). In this study I have attempted a review of the issues under debate with the purpose of stating the problems. This has included a new interpretation of existing, and new, fossil specimens, proposed in common with K. S. W. Campbell and reported separately.

Historical

Denison (1968), commenting on the evolutionary significance of the earliest known lungfish *Uranolophus*, recognised that the scattered, conical denticles were primitive and noted the absence of both teeth and tooth plates. He accepted that the dentition of lungfishes was unique in the absence of marginal tooth-bearing bones and considered, as Westoll (1949) had, that the primary evolutionary shift was in response to new feeding methods, resulting in a relatively rapid change in the dentition. Consequently some genera evolved tooth plates and others retained the scattered denticles but evolved, in addition, what Denison (1968) termed " tooth ridges " at the margins of the palatal bones.

Since 1968, and the Nobel Symposium on " Problems of Lower Vertebrate Phylogeny ",

Source : MNHN, Paris

TABLE 1. (Modified from Denison, 1974, p. 32). The headings " Denticles present " and " Teeth evolved " have been created from Denison's comments in the text, and *Speonesydrion* and *Stomiahykus* added as new genera. *Holodipterus* could also be placed in the " Teeth evolved " column. Two non-Devonian genera have been added.

Devonian Genera		
Dental Plates Present	Dental Plates Absent *Dipnorhynchus sussmilchi*	
	Denticles Present	Teeth Evolved
Chirodipterus *Conchodus* *Dipterus* *Oervigia* *Palaeodaphus* *Rhinodipterus* *Scaumenacia* *Sunwapta* *Stomiahykus*	*Fleurantia* *Griphognathus* *Holodipterus* *Uranolophus* *Conchopoma* — U. Carb.	*" Dipnorhynchus " lehmanni* *Speonesydrion iani* *Ganorhynchus splendens* *Uronemus* — M. Carb.

there has been a rapid expansion of knowledge of early forms of dipnoan and many reviews of the dentition by Denison (1974), Miles (1977), Smith (1977) and Campbell & Barwick (1983, 1986). Resulting from Denison's (1974) analysis of dipnoan dentitions, it has been generally accepted that two categories exist, tooth-plated and non-tooth-plated. However, Denison did not regard his groups as having any taxonomic significance. The group without toothplates was a repository for types with very diverse dental adaptations. Campbell & Barwick (1983), however, while regarding Denison's division into tooth-plated and non-tooth-plated forms as an artificial one, still maintained a division based on dental types which they called the rasping, denticulated type and the triturating, tooth-plated type. They suggested that these two groups represented two divergent evolutionary lines resulting from very different modes of feeding. Within the tooth-plated group, Campbell & Barwick (1983, p. 45) included *Dipnorhynchus*, a genus with formless crushing surfaces, and one not included by Denison in his genera with dental plates (Table 1). The inclusion of *Dipnorhynchus*, as a genus with a primitive tooth-plated dentition, is a return to ideas previously proposed by White (1966) and Thomson (1965, 1967), that this type with dental plates is not preceded by a toothed, denticulate stage.

Contrary to these views, Denison (1974) suggested that tooth plates had arisen from a plateless primitive condition where scattered denticles were shed and replaced, to one in which denticles were retained, arranged in rows, and enlarged. The concept expressed here by Denison, is that denticles contribute to development of the tooth plate, both in ontogeny and phylogeny, some being retained, while also becoming larger and aligned into rows in predetermined positions. Denison (1974, p. 55) made no attempt to distinguish teeth from denticles in this account of the evolution of what he called dental plates. Denison (1974, p. 56) also suggested that dental plates may have arisen more than once from denticulated forms.

Miles (1977, p. 296), in the most comprehensive review of lungfish phylogeny, accepted Denison's view that the primitive dentition consisted of a shagreen of shedding denticles, for the principal reason that this condition is primitive for gnathostomes. Campbell & Barwick (1983, p. 47) did not agree with this view but considered shedding denticles to be secondary to retained denticles, on the assumption that " crushing dentitions " (implied dental plates) are the primitive condition, developed in ontogeny from retained denticles, after wear, giving rise to sheets of continuously growing dentine. Unlike Denison, who had interpreted marginal tooth ridges as a derived character, Miles proposed that tooth ridges are part of the primitive dentition for dipnoans and had evolved only once; he also proposed that lungfishes with organised tooth plates are a monophyletic group, the most primitive representative of which is *Dipterus valenciennesi*.

The recent discovery of two new early Devon-

Source : MNHN, Paris

ian fossil genera has emphasised the problem of the lack of agreement on interpretation of dental characters. One is *Diabolepis speratus*, (Chang & Yu, 1984) from the Lower Devonian of Eastern Yunnan, China, which Chang & Yu concluded, forms the sister-group of all previously described dipnoans. This provides the best available outgroup comparison for dipnoans. The second is *Speonesydrion iani* Campbell & Barwick (1983), from the Lower Devonian of New South Wales, which Campbell & Barwick (1983, 1984) described as a primitive dipnoan sharing a large number of characters with *Uranolophus* and *Dipnorhynchus*, but closer to the latter. According to Campbell & Barwick (1983, p. 45) the three oldest genera of dipnoans, *Uranolophus*, *Dipnorhynchus* and *Speonesydrion*, share primitive characters that suggest a powerful bite, but they concluded that the primitive dipnoan had dental plates of continuously growing dentine as in *Dipnorhynchus* and *Speonesydrion*. This conclusion was based on the supposition that plates of continuously growing dentine were better adapted than small shedding denticles to a mode of feeding in which crushing with powerful muscles was assumed to be the primitive condition. Several features are important in these descriptions of early Devonian genera. In *Speonesydrion iani*, Campbell & Barwick (1983, 1984) described teeth arranged in radial rows, separated by radial groves, similar to the morphotype of a radiate tooth plate. They concluded that this form is primitive for all those dipnoans with radiate tooth plates as in *Dipterus valenciennesi*. In a paper describing a new species of *Dipnorhynchus*, i.e. *D. kurikae* Campbell & Barwick (1985), Campbell & Barwick (p. 314) acknowledged that the dental plates of *Speonesydrion* and *Dipnorhynchus* are similar in that they grew partly by the incorporation of new marginal denticles, but are different in that those of *Speonesydrion* also grew by the addition of "prominent teeth" at the lateral margins. Accepting that one can distinguish two different types of dental plates, dentine plates and tooth plates (Smith & Campbell, 1987), Campbell & Barwick (1985, p. 314) concluded that *Speonesydrion* is the earliest known member leading to tooth-plated types, and *Dipnorhynchus* is the earliest of the dentine-plated types. This statement makes no acknowledgement of which of the two is the more primitive and specifies that if both are members of the Dipnorhynchidae, it is a grade group, in which dental plates are paraphyletic. I consider that the important feature of the dentition in *Speonesydrion* is the presence of large, conical teeth at the lateral margins of the ridges of the tooth plate and that *Speonesydrion* may be the earliest dipnoan in which separate conical teeth can be recognised. How these teeth may have differentiated in ontogeny of the tooth plate will be debated in this paper, because Campbell & Barwick (1984, p. 41) have concluded that the teeth arise by enlargement of some of the marginal denticles. I would dispute this on the basis that the primitive gnathostome dentition had the potential to form both teeth and denticles, and that it may be necessary to distinguish between the two.

Returning to the description of *Diabolepis*, Chang & Yu (1984, figs. 4 and 5) described the pterygoid and prearticular as tooth-plate-like with a covering of flattened teeth in regular rows, but the account and illustrations do not show that a row of teeth fuses into a ridge alternating with a groove, in a way common to many dipnoan tooth plates. However, the opposing tooth plates are described as having reciprocally curved surfaces which may be a significant feature of early dental plates. Although large teeth are described in *Diabolepis* these are present on the anterior part of the parasphenoid, with small irregular teeth behind, and not at the lateral margins of the dental plates as in *Speonesydrion*. My interpretation is that *Diabolepis* does not have the arrangement of the dentition that would allow it to be closely related to the early dipnoans with primitive dental plates[1].

Observations

Three areas of uncertainty arise from this survey of the literature:

1) the concept of tooth plates, with the implication that they develop, both in ontogeny and phylogeny, from radially arranged teeth. However, the term is used interchangeably with dental

1 Smith and Chang (in prep.) conclude that *Diabolepis* does have tooth plates of a primitive dipnoan type.

Source : MNHN, Paris

plate to include flat dentine sheets of one type found in *Dipnorhynchus*, in which teeth have never been found. I propose that tooth plates and dentine plates should be the terms used for dentitions that may be independently derived along two or more lines of evolution amongst genera with dental plates, and that the divergence between them occurred early in the Devonian. The morphological evidence for this will be discussed in this paper;

2) the concept that tooth ridges in three genera, *Uranolophus*, *Griphognathus*, and *Uronemus* are homologous structures, as Miles (1977, p. 297) proposed. This feature of the dentition will also be briefly considered in this paper with regard to *Uronemus*;

3) the concept that the primitive condition consists of scattered shedding denticles; although the presence of scattered denticles is accepted as the primitive gnathostome condition (Miles, 1977; Reif, 1982) it is not known whether primitively in dipnoans they were shed and replaced, or whether primitively they were retained and overgrown by superpositional growth, as happens in the dipnoan dermal skeleton (Smith, 1977, p. 62). Miles (1977, p. 297) considered that shedding was the primitive state for dipnoans. Campbell & Barwick (1983, p. 45, 1986) considered that retained and shedding were "equally ancient" conditions for dipnoan dentitions. Few observations made in this paper make any substantial contribution to this aspect, and it is not intended to comment further.

In this paper I should like to consider first whether or not a distinction can be made between teeth and denticles in both extant and fossil forms, and if so how this could be achieved. Second, how do these structures contribute to the ontogenetic and phylogenetic development of dental plates? As suggested above, I will use the general term dental plate to include both types, dentine plates and tooth plates, acknowledging only that the dentition of these types is of a composite type and does not have separate shedding teeth and denticles as in other gnathostomes (Fig. 1).

It is assumed, first that knowledge of patterns of development and growth in morphogenesis of the dentition can make a significant contribution; second, that attempts to interpret ontogenetic history and growth from the analysis of structure in fossils, can both make a valid contribution to evolutionary biology. This can be achieved by extrapolation from a static, graded series, and from the record in the hard tissues of stasis and growth, in continuously growing dental structures.

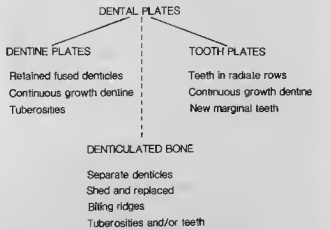

FIG. 1. — Proposed new terminology of two types of dental plates in dipnoans; dashed line shows third group: those without dental plates or denticulate forms.

A. *Distinction between teeth and denticles*

In the accounts of dipnoan dentitions discussed above, the term denticle has been used for small structures in the oral cavity; further distinction is made on the basis of whether they are retained or shed, or their distribution is scattered or marginal. Larger structures have been called teeth, sometimes tusks, and if associated with dental plates, they have been referred to as cusps. In the account of the dentition of *Diabolepis speratus*, Chang & Yu (1984, p. 176) referred to small irregular teeth, low-crowned teeth and large teeth, but not denticles. Campbell & Barwick (1983, 1984) while referring to teeth and tooth rows in tooth-plated genera, clearly regarded the teeth as a special modification of marginal denticles (Campbell & Barwick, 1985, p. 314). There is a need to consider a better distinction; one based on size alone is not sufficient because teeth start small in early stages and get larger in the adult.

Assuming different developmental pathways, one can propose a developmental definition. Reif (1982, p. 291) attempted to distinguish dermal

Source : MNHN, Paris

denticles in the oral tissues from teeth in this way: denticles develop superficially " on demand " or when space allowed; teeth develop from a deep epithelial invagination (dental lamina) providing a permanent tooth generative structure from which successive teeth developed. Replacement teeth are prefabricated in advance of the old teeth being shed. This provided the possibility of larger teeth, preformed prior to requirement and prior to available space, restricted to specific locations (teeth loci) in the jaws, and formed at predetermined but variable intervals; the tooth primordium (protogerm), giving rise to a tooth family, often made of teeth of similar shape but increasing size.

Reif (1982, p. 291 and 348) modified Orvig's (1977) definition of an odontode, the unit of both dermal and oral skeleton, and accepted that teeth and oral denticles were two kinds of odontode. Each odontode is the product of one set of interactive, inductive stimuli, between dental epithelium and dental mesenchyme; for teeth, these together form the tooth primordia (protogerms, Reif, 1982, p. 292). Any morphological changes in the teeth, their shape, size, pattern and timing of initiation are controlled by differentiation events in the tooth primordium. Reif (1982) further proposed a model for vertebrate dentitions in which *in situ* replacement of denticles, developing only when a space occurred, was substituted by a system where teeth develop from a dental epithelium (lamina), whose continued growth, away from the superficial odontogenic epithelium, provides inhibition-free areas for automatic induction of teeth (Reif, 1982, p. 349). He proposed that all gnathostomes, except placoderms, possess a dental lamina, and therefore, teeth are primitive for all these taxa. The primitive condition for all gnathostomes except placoderms, is scattered, shedding denticles, and teeth.

I propose that the arrangement of dental structures can be used to determine their locus of development from a series of fossil specimens, and that this allows the distinction to be made between teeth and denticles. New teeth (conical enamel covered structures) are located at specific sites, relative to older ones, and have formed at predetermined time intervals from a tooth primordium. Examples with teeth are *Speonesydrion iani*, *Holodipterus gogoensis* and *Uronemus splendens*. The dentine is specialised in more derived forms (petrodentine Smith, 1984). Denticles, by contrast, are located over all surfaces and are replaced randomly, wherever oral epithelium has covered the bone surfaces, above and between existing denticles and in sites where denticles have been shed; the dentine is simple as in *Griphognathus* (Smith, 1977, p. 38). Based on this proposal, it is suggested that dipnoan dentitions comprise four basic types:

1) those with teeth and denticles; both were shed, as in *Fleurantia*, or teeth were shed and some denticles retained as in *Holodipterus*;

2) only shedding denticles, the marginal ones fused into biting ridges before shedding, as in *Griphognathus*;

3) denticles which are retained together with retained teeth, as in *Speonesydrion*;

4) only denticles which are retained and fused into continuous sheets of dentine, as in *Dipnorhynchus*.

As suggested above, the term " dental plate " is used to include two distinct types; a) *dentine plates*, formed by fusion of retained denticles and addition of numerous groups of denticles, mainly to the lateral and postero-lateral margins; b) *tooth plates*, formed by teeth arranged in radiate rows, retained and worn into tooth ridges (Fig. 1). Addition of teeth is at the lateral margin of each radiate row, some of which may be antero-lateral or postero-lateral.

B. *Growth of dental plates*

As early as 1917, Stromer & Peyer (1917, Fig. 3) figured sections through several types of dipnoan dental plate to show how, in ontogeny and in adult growth, teeth (as in *Dipterus tuberculatus*) or marginal and basal tissue (as in *Ceratodus runcinatus*), were added laterally to each ridge. Similarly, in Fig. 2, it can be seen how growth increments are added, and how distinctive separate teeth contribute to the structure of each ridge. Thomson (1965, p. 241) commented on the growth of adult dental plates in *Ctenodus*, *Tranodis* and Devonian genera and noted that growth of the ridges is effected by addition of new " denticles " to the outer rim, and by thickening of the basal part. He further suggested

Source : MNHN, Paris

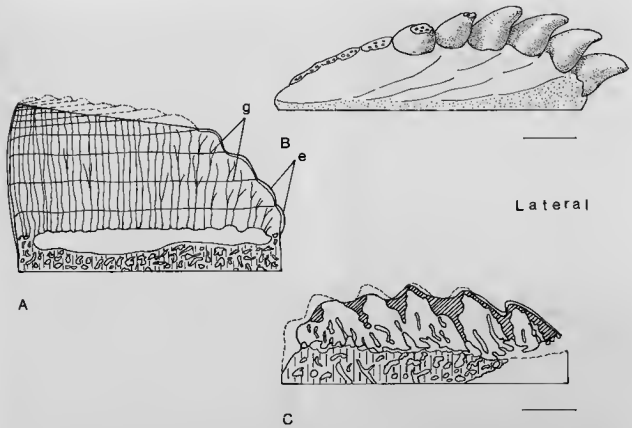

FIG. 2. — Diagrams to show profiles of dental plates and the addition of teeth or new tissue at the lateral margin. A, Schematic diagram of a vertical, medio-lateral section of *Ceratodus runcinatus*, showing growth lines (g) and lateral enamel-covered increments (e); dashed line represents surface before wear and loss of tissue (after Stromer & Peyer, 1917). M. Triassic, approx. × 2; B, Profile view of first ridge in *Dipterus* sp., Antarctic, U. Devonian, AM-F54323-4, to show progressive addition of separate larger teeth. Bar = 1 mm; C, Vertical, medio-lateral section through juvenile *Ceratodus parvus*, showing columns of petrodentine centrally within each tooth (after Peyer, 1968, fig. 63, & plate VIe). Bar = 1 mm.

that the pattern of growth was by increase in size and number of the " denticles ", as this was also true for the phylogenetic sequence. Denison (1974, p. 39) commented on this growth in *Dipterus*, and described new " larger denticles " added laterally to each ridge. He also figured (Denison, 1974, fig. 5) a section through *Scaumenacia* showing separate, large, unworn teeth, referred to as " denticles ", at the lateral extremity of one radiate row of the tooth plate. Similarly, a section through one ridge of *Sagenodus* (Denison, 1974, fig. 7) showed the addition of a new " denticle " at the lateral margin. Following the same terminology, Smith (1979) described the histogenesis of the new tissue, and the way in which in areal growth each new " denticle " provided another column of petrodentine to add to that already growing beneath the worn ridges. As the worn " denticles " were later referred to as cusps by Denison (1974), it is clear that no distinction was made between denticles and teeth. The dentitions of *Dipterus*, *Scaumenacia* and *Sagenodus* fit the definition of tooth plates given above and are therefore examples of tooth plates and not dentine plates. However, the adult plates of *Ceratodus runcinatus*, *Ceratodus kaupi* and other ceratodontids do not appear to grow by the addition of separate teeth (Stromer & Peyer, 1917; Smith, pers. obs.), and can only be included as tooth plates (sensu Smith this paper) if it is assumed that their ontogeny is the same as that of *Neoceratodus*. Phylogenetic change would have been through alteration of the developmental strategy.

It is known that the developmental basis for the morphology of adult tooth plates in extant

Source : MNHN, Paris

lungfishes is initiation of small teeth in a radiating pattern of short rows (Smith, 1985, fig. 15); although Kemp (1977, 1979) referred to these as cusps and Smith (1985) retained the term "denticle". Smith (1985), using serial sections of *Protopterus aethiopicus*, considered that a lateral extension of the dental epithelium at the base of each "denticle", together with adjacent dental mesenchyme, constituted a protogerm (Smith, 1985, figs. 3 and 10C), for the initiation of a new "denticle". This was only found at the lateral margins of the rows, deep to the superficial epithelium, and was assumed to represent a dental lamina. Dental plates in both extant genera form by the fusion of separately differentiated elements, homologous with odontodes (Smith, 1985, fig. 15) and not by differentiation of cusps within a tooth-plate anlagen. Kemp (1977, 1984, p. 260) also considered that the dental plates of larval lungfishes formed by the fusion of isolated "denticles" in radiate rows, because she described the members across the ridge-rows as being part of a tooth family (Kemp 1977, fig. 1), although she referred to them as cusps (1977, p. 237, 1979, p. 255, p. 281). It is clear from these accounts that although the earliest "denticles" to develop may be superficial, they are located in precise positions and all subsequent ones develop at specific loci from a sub-epithelial dental epithelium and are in these respects the same as teeth. Because they are also arranged in organised radiating rows the whole structure is considered to be a tooth plate.

Many examples of fossil juvenile tooth plates also show radiate rows of small teeth, becoming worn into ridges as in *Sagenodus* (Lund, 1969) and *Monongahela* (Lund, 1973; see Smith, 1985, p. 640 for discussion), and in *Dipterus sp.*, (Fig. 3) (material supplied by P. Janvier form the Zaab valley, E. Turkey).

A problem exists in accepting that the proposed model for ontogeny and growth of the dentition is true for all dipnoans with tooth plates because the adult tooth plates of *Neoceratodus* and *Protopterus* do not grow by the addition of separate teeth to each ridge ; unless we accept that the adult plates of the more derived forms no longer grow by the addition of separate teeth but by layers of dentine added to the base, extending the plate laterally. This is often marked by a slight elevation of the enamel-covered lateral margin as shown in *Ceratodus runciatus* (Fig. 2) (Stromer & Peyer, 1917, fig. 3F; Smith *et al.*, 1984, fig. 1), in *Neoceratodus* (Kemp, 1979, figs. 12 & 14) and in *Protopterus aethiopicus* (Bemis, 1984, figs. 5 & 8; Smith pers. obs.). It would appear difficult to accept a definition of tooth plates based on growth of the adult ones in the extant lungfishes (clearly this needs to be resolved) but this difficulty is not a reason to abandon the proposed model because many of the fossil adult

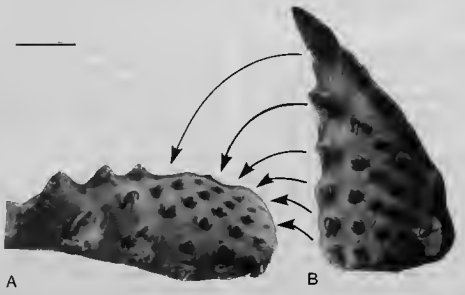

FIG. 3. — SEM's of juvenile tooth plate of *Dipterus* sp. from the Zaab valley, E. Turkey (U. Devonian). Lines show the equivalent tooth rows in each view. A, Dorso-lateral view; B, Dorso-medial view. Bar = 0.4 mm.

Source : MNHN, Paris

plates do show the addition of teeth to the lateral margin with increasing size of the teeth. It can be assumed from these data on extant forms that all forms of radiate tooth plate develop in ontogeny by the fusion of teeth, arranged in radial rows. These data are reinforced by the few very small juvenile tooth plates found in *Dipterus*, *Sagenodus*, and *Monongahela*. However, other types of dental plate exist, i.e. dentine plates, which may not develop in this way, and juvenile stages of these have not been recognised as such in fossil specimens.

C. *Tooth plates*

Although Denison (1974, p. 32) used a table as modified in Table 1, with genera listed as " dental plates present or absent ", throughout the text he mainly referred to tooth plates, and both terms were used synonymously. Clearly all Denison's genera with dental plates had what Miles (1977) regarded as organized tooth plates; i.e. plates separated medially with radial ridges continuing into tooth-like structures at the lateral margins. White (1966) had also used the terms interchangeably, although he noted that the toothed ridges became less toothed in the later species, for example *Neoceratodus*. Denison (1974, p. 35) excluded the dentition of *Dipnorhynchus sussmilchi* from those with tooth plates and described it as a crushing dental plate of raised blisters. However, pertinent to this discussion is the observation (White, 1966, p. 7) that in *Dipnorhynchus lehmanni* there was a tritural surface and an indication that teeth had formed, if of a rudimentary kind. The new genus *Speonesydrion iani* fits into this category (probably *D. lehmanni* is congeneric), and the suggestion (Campbell & Barwick, 1984, 1987) that the dentition is primitive for all those with tooth plates is accepted. However, I accept this not for the reason that continuously growing sheets of dentine are better adapted than shedding denticles for a crushing function, but because I consider the dentition to be generalized in the possession of four basic components; these are shown in Fig. 4:

1) radially arranged teeth, the newest and largest being the most lateral;

2) teeth which merge into radial ridges formed of worn tooth bases (Campbell & Barwick 1983, figs. 9 and 10);

3) vermiform denticles between the ridges covering the furrows, with wear from the opposing plate interlocking " ridge to furrow ";

4) postero-medially the ridges run into a raised blister of smooth dentine forming a crushing heel to the tooth plate of the prearticular, apparently as a postero-medial extension of the ridges. However, Campbell & Barwick (1984, figs. 29 & 30) believed that the heel formed by retention of scattered denticles and fusion into a continuous sheet of dentine growing by apposition against the underlying bone. They deduced a similar mechanism of growth for the dental plate of *Dipnorhynchus sussmilchi*. While it is certainly true that increase in area at the lateral margins of *Speonesydrion* was by the addition of discrete teeth, (Figs. 4B, C) and also clusters of retained denticles (Campbell & Barwick, 1983, figs. 10A, C), it is not clear how the postero-medial portion of the plate grew.

The dentition of *Dipterus valenciennesi* has been proposed by Miles (1977, p. 299) as the primitive form with radiate tooth plates, all other forms with tooth plates being derived relative to this, with increasing complexity of the dentine and enlargement of the pulp chamber. He concluded that the ultimate specialization of petrodentine was not reached until the lepidosirenids. However, Smith (1984, p. 394) showed that petrodentine can be demonstrated in the teeth of *D. valenciennesi* from the Middle Devonian and all tooth plates of post-Devonian genera, and proposed that it is a derived character found in all dipnoans with radiate tooth plates. *Speonesydrion* would therefore be a primitive form with radiate tooth plates in which petrodentine had not developed.

New data on the dentition of *Uronemus*, a Carboniferous genus, show that this form has a highly derived tooth plate (Smith, Smithson & Campbell, 1987). Based on this, *Uronemus* is removed from the group lacking tooth plates and placed among those with radiate tooth plates. Previously, *Uronemus* had been considered by Miles (1977) as allied to those with the primitive dentition of denticles and biting ridges; accepting Smith *et al.*'s (1987) conclusions, it can be placed on the cladogram (Miles, 1977, fig. 157) between

Source : MNHN, Paris

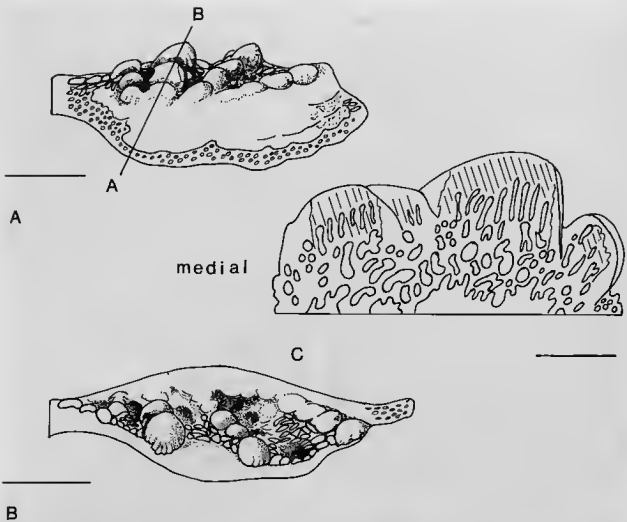

FIG. 4. — *Speonesydrion iani* ANU 35648, & CPC 103041. A, left tooth plate, medial view. A-B line equivalent to position of vertical section in C; B, right tooth plate, dorso-lateral view, shows newest large teeth and vermiform denticles in the furrows (both after Campbell & Barwick, 1984, figs. 30B, D). Bar = 10 mm; C, vertical, medio-lateral section in plane A-B in A, shows addition of enamel-covered teeth to lateral margin, and position of regular dense dentine within the body of each tooth (part of the medial tissue is missing in this fragment). Bar = 2 mm.

Dipterus and *Ctenodus*. These conclusions were made on the basis of several characters present in tooth-plated forms. In particular, teeth were added laterally, became more worn medially, and each tooth possessed petrodentine within the pallial dentine which grew into the bone to contribute to the wear resistance of the tooth ridge. The most important observation was that wear pits are present in positions between the radial rows of teeth, suggesting closely interlocking, opposing plates. The marginal ridge, formed by wear of the teeth in one elongated lingual row, was therefore considered not to be homologous with the biting ridges of *Uranolophus* and *Griphognathus*, as originally proposed by Miles (1977, p. 297), but to be part of a highly modified tooth plate.

D. *Dentine plates*

These are considered to be different from tooth plates because true teeth never develop and never contribute to the plate. Instead the mar-

Source : MNHN, Paris

gins grow by the addition of fields of denticles, of a type exemplified by those of *Dipnorhynchus* (Fig. 5), and illustrated by Campbell & Barwick (1983, fig. 3).

Specimens of *Chirodipterus australis*, from the Gogo Formation in W. Australia, provide excellent morphological and histological detail of denticle growth and wear at the margins of the dental plate. Miles (1977, p. 165 & 291) described the detailed morphology of the dentition in *Chirodipterus australis* as typical of highly organized, paired tooth plates, and Smith (1977, p. 50) described several unique aspects of the histology of the dentine and the marginal tissue. In order to resolve some outstanding problems, Smith & Campbell (1987) reinvestigated the dentition of *Chirodipterus* and have concluded that the plates are significantly different in their growth and justify their inclusion in a new category, i.e. dentine plates. These new observations show that the increase in area to the dentine forming the main mass of the tooth plate is achieved by the addition of groups or stacks of blister-like denticles to the lateral margins (Fig. 6). The tuberosities found at the ends of the short radial ridges are not considered to be homologous with teeth, because they are never enamel-covered, and never develop as new structures at the extreme margin of the plate, but always arise a short distance in from the plate margin, first as low elevations of petrodentine. It is the enamel-covered denticles that are the newest structures at the margins of the plate. The tuberosities, it is concluded, arise by differential growth and wear of the petrodentine and the primary trabecular dentine. This method of growth is different from that of radiate tooth plates, and has led to a distinction between two fundamentally different types of dental plate. Many other genera have dentine plates similar to those of *Chirodipterus*, in particular *Sunwapta* and *Stomiahykus*. All these genera should be grouped together on the basis of their dentition. It is of some interest that Pander in 1858 (Plate 7, figs. 10A-E) illustrated stacked-up rows of blisters at the plate margin of *Dipterus glaber*. He commented that these " tubercles " were in various stages of development and wear and that they were gradually built into the ridges of the plate. This is exactly the mechanism that we have proposed (Smith & Campbell, 1987) for continued growth of dentine plates from stacks of denticles.

E. *Pseudo-plates*

Using newly prepared material, the dentition of *Holodipterus* has been compared with examples of tooth-plated and denticulated types (Campbell & Smith, 1987) as in *Speonesydrion* and *Fleuran-*

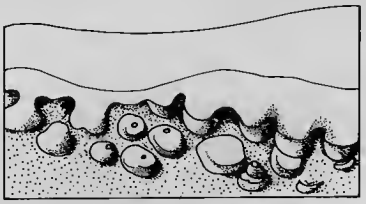

FIG. 5. — *Dipnorhynchus sussmilchi* ANU 18815, early Devonian, palatal dental plate (trilural surface at the top). Lateral margin of posterior two thirds showing addition of enamel-covered denticles to deep lateral border; shows growth line in fused dentine sheet and advancing edge encroaching on denticulate area (see also Campbell & Barwick, 1983, fig. 3). Bar = 2 mm.

Source : MNHN, Paris

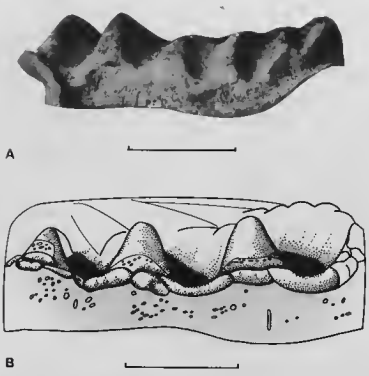

FIG. 6. — *Chirodipterus australis* P56042 & P52564. A, lateral view of a prearticular dental plate to show stacks of blister-like denticles following the undulations of the plate margin, with larger ones adjacent to the ridge ends. Bar = 5 mm; B, drawing of a lateral view to show how enamel-covered denticles add to the margin of the plate and become worn medially as they merge with the tuberosities of the ridge. Bar = 4 mm. (See Smith & Campbell, 1987, figs. 28 and 32B).

tia (Campbell & Barwick, 1983). After a detailed analysis of macromorphology and histology, relationships of *Holodipterus* with either group could not be conclusively demonstrated (Campbell & Smith, 1987) although Campbell considered that *Holodipterus* belonged to the denticulated group because most of the characters of the feeding system are shared with that group. I favour an alternative explanation that *Holodipterus* has retained a primitive dentition of teeth and denticles, simulating a tooth plate (pseudoplate), retaining teeth for long enough to form short radiate rows at the margins of the palate and lower jaw (Fig. 7) as in a tooth plate (Campbell & Smith, 1987, figs. 3, 4A, 6 and 7), also by retaining marginal denticles lateral to the teeth, as in *Speonesydrion*. Later waves of resorption removed the older worn teeth and medial denticles. Miles (1977, p. 298) considered that this arrangement of teeth in *Holodipterus* " prefigures " the radiating rows of ridges in the tooth plates of many forms. I agree that they are rudimentary tooth-rows but consider it as a derived form relative to *Speonesydrion*, a type not known at the time Miles produced his review.

The teeth of opposing plates interlock around the lateral margins, as they appear to have done in *Speonesydrion*. The morphology of the dentition is different from individual to individual because of the resorption and repair which reconstructs the dental tissues, a process that is a derived condition for *Holodipterus*. New teeth were added to each short row at the lateral margins in advance of denticles which formed later to buttress the tissues around the tooth base (Fig. 7A), acting as an occlusal stop to the opposing teeth, as in *Speonesydrion* (Campbell & Barwick, 1984, figs. 29, 30).

In summary, I agree with Miles (1977, p. 279) that *Holodipterus* may have retained a primitive arrangment of the dentition and reject his further suggestion that it is functionally derived. Campbell & Barwick (1986) thought that *Holodipterus* is a derived form related to the denticulate lineage but I (Campbell & Smith, 1987) was

Source : MNHN, Paris

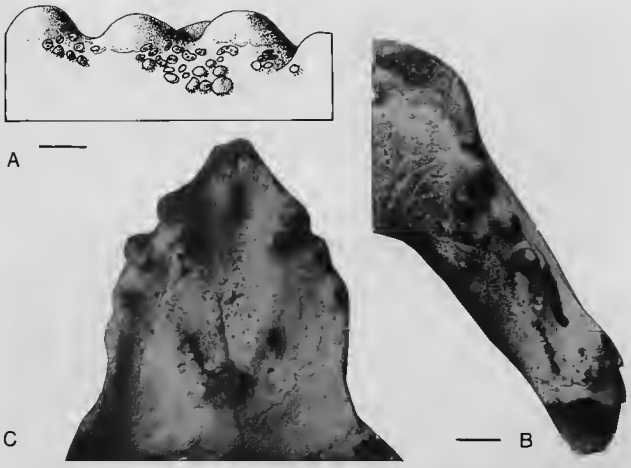

FIG. 7. — *Holodipterus gogoensis*, P52569. A, Lateral view of mandible in B to show the arrangement of small worn denticles in clusters on the steep lateral border of the tooth tows. Bar = 5 mm; B, Postero-dorsal view of the right mandible, not whitened with NH Cl, shows the position of the three large teeth as separate structures at the lateral border. Bar = 10 mm ; C, Ventral view of palate to show the position of the three teeth on each side, the first two rows on the left and the first on the right have a second inner tooth. Small scattered denticles cover the entire palate, many submerged in an investing layer of bone ; P56045. Bar = 10 mm. (Campbell & Smith, 1987, figs. 4 & 7).

unable to agree with this interpretation because I consider that *Holodipterus* is derived from the *Speonesydrion* type. Campbell & Smith (1987) reported that a type of dentine, apparently similar to petrodentine, is present in the teeth of *Holodipterus*. This fact makes it necessary to assume that this special tissue type developed independently in this genus from that in *D. valenciennesi* although it may be present in an as yet unknown fossil intermediate between *Holodipterus* and *Speonesydrion*.

INTERPRETATION

The condition in *Speonesydrion* is assumed to be primitive for dipnoans with dental plates and generalized because four features (Fig. 6), described in the previous section, could contribute directly by supression or enhancement, to at least two types of dental plate. It is primitive for the reason that both teeth and denticles are present, that being the primitive gnathostome condition (Reif, 1982). The best illustration of teeth and denticles in *Speonesydrion* is by Campbell & Barwick (1983, fig. 10). Dentine-plates of the type found in *D. sussmilchi* could be derived

Source : MNHN, Paris

from a type represented by *Speonesydrion iani*, by the supression of teeth, at least in the adult, and the fusion of all denticles, to form a continuous sheet of dentine. Campbell & Barwick (1984, fig. 32) have shown that in the smallest specimen of *Speonesydrion*, the tooth plates are relatively smooth, without ridges or marginal teeth and with only irregular shaped denticles contributing to the growth of the lateral margin. Dentine plates could, therefore, have arisen in phylogeny by a process of paedomorphosis. Bemis (1984b) has suggested that paedomorphosis was extensive in the evolution of lungfishes and has concluded that it is a reasonable explanation for many of the derived morphological characters. In the dental plates of *Dipnorhynchus*, only denticles remain at the growing margins of the plates (Fig. 5), also figured by Thomson & Campbell (1971, figs. 18 and 20) and Campbell & Barwick (1983, fig. 3). This feature is one proposed as a characteristic of dentine plates and *D. sussmilchi* would fit into this category. The dental characters of *Dipnorhynchus sussmilchi* are therefore derived, and in this respect I agree with Denison (1974, p. 35) that this is a specialised adaptation. Miles (1977), noted that there were traces of the primitive dentition in the nodose surface at the postero-dorsal corner of the prearticular. The dentition of *D. lehmanni*, although poorly preserved, would appear to be intermediate, in the possession of a poorly differentiated dentition with simple knobs (teeth), between those of *Speonesydrion* and *D. sussmilchi*. The distribution of "teeth" on the palate is shown in a reinterpretation by Campbell & Barwick (1984, fig. 3). I propose that the polarity of these character-states is from that of *Speonesydrion iani* to that of *D. sussmilchi* because I assume that the dentition changes by regression from the generalized condition to the specialized one. However, Campbell & Barwick (1983, p. 313) proposed that *D. lehmanni* shows the primitive condition of the dentition because it is stratigraphically the oldest (Siegenian as opposed to Zlichovian). They also acknowledged that the concept of crudity of the dentition has no validity for determining primitiveness. They further suggested that dental structures have greater value than roofing bone patterns, but while acknowledging the similarity of the dental complex of *Speonesydrion* and *Dipnorhynchus sussmilchi*, they considered that the prominent teeth of *Speonesydrion* presage organised radiate tooth plates. For this reason they concluded that *Speonesydrion* cannot give rise to the dentine plates of *Dipnorhynchus sussmilchi* and is the most primitive example of a tooth-plated lineage. With this statement, they acknowledged that the "crudely differentiated surfaces" of *D. sussmilchi* are equally as primitive as those of *Speonesydrion* because they are first in a lineage of dentine-plated genera that are paraphyletic with tooth-plated types.

I also accept that the plates of *Stomiahykus* and *Chirodipterus* are related to those of the dentine-plated types as suggested by Smith & Campbell (1987) and Campbell & Barwick (1986, p. 314). All these taxa based on the dentition alone would form a group which is the sister-group of all tooth-plated dipnoans. I have no comment to make on the relations of all those with dental plates to the denticulate genus *Uranolophus*. While acknowledging that *Holodipterus* has neither typical tooth plates nor typical dentine plates, it may be more closely related to *Speonesydrion* than to any of the denticulate genera. Only a full character analysis will resolve whether this is true or not.

From analysis of the dentition of *Uronemus splendens* on the basis of the characters present in tooth-plated forms, as proposed in this paper, we concluded (Smith, Smithson & Campbell, 1987) that this genus is a derived form from the *Speonesydrion-Dipterus* type. As previously discussed, this places *Uronemus* at a different node on the cladogram of Miles (1977) and resolves many problems, as stated by Bemis (1984b, p. 304), when several features of *Uronemus* were not congruent with his proposed cladogram, in particular character 7, tooth plates.

Conclusion

Two distinct categories of dental plates exist; 1) *dentine plates*; and 2) *tooth plates*. Analysis of those specimens of fossil genera suitable for macroscopic and microscopic investigation indicates that at least two divergent lineages exist. The morphotype depicted by *Speonesydrion* is considered to represent the primitive condition for all genera with radiate tooth plates, as suggested by Campbell & Barwick (1984), and

Source : MNHN, Paris

may also lead to the type of dentition in *Holodipterus*. It is probable that it is also primitive for those with dentine plates, such as *Dipnorhynchus sussmilchi*, although Campbell & Barwick (1984, p. 46) do not think this is true. Of the other genera with dentine plates, *Stomiahykus thlaodus* is considered to be a morphological intermediate between genera such as *Speonesydrion* and *Chirodipterus*, and *Sunwapta grandiceps* is the closest species to *Chirodipterus australis* (Smith & Campbell, 1987).

It may not be necessary to stick ridgidly to the definitions of tooth plate and dentine plate proposed in this paper, because the terms have generally been used simply to indicate a dentition different from that of many gnathostomes in that separate marginal teeth are not present. However, I suggest that there is a real difference in the way the types of dental plates have evolved, and this should be considered in any analysis of relationships amongst dipnoans.

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Abbreviations

A.N.U. Geology Department, Australian National University, Canberra, A.C.T., Australia.
C.P.C. Commonwealth Palaeontological Collection, Bureau of Mineral Resources (Geology and Geophysics), Canberra. A.C.T., Australia.
P. Palaeontology Department, British Museum of Natural History, London.

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Source : MNHN, Paris

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Source : MNHN, Paris

New Mississippian Holocephali (Chondrichthyes) and the Evolution of the Holocephali

R. LUND

ABSTRACT

A restoration of *Echinochimaera meltoni* with additional information on the occipital spines and structure of the pectoral fin is presented. *Echinochimaera snyderi*, nov. sp., differs from the type species in having a successional upper anterior tooth family as well as in characters of the jaw plates and first dorsal fin. The new species *E. kellyi*, *E. sulphurea*, *E. indiana*, and *E. elusiva* are described from isolated jaw plates from the Chesterian of Indiana. The morphology and mode of growth are contrasted with recent chimaeroids and several ontogenetic stages of cochliodonts. The Mississippian jaw plates closely resemble those of *Echinochimaera*, and are derived relative to the jaw plates of either chimaeroids or cochliodonts, while the plates of recent chimaeroids may most reasonably be derived from a juvenile stage of a cochliodont tooth plate by paedomorphosis. On the basis of the available evidence, Echinochimaeroidei are the sister-group of the Chimaeroidei, and Chimaeriformes are the derived sister-group of the Cochliodontiformes.

RÉSUMÉ

L'auteur présente une reconstitution d'*Echinochimaera meltoni* comportant des informations supplémentaires sur les épines occipitales et la structure de la nageoire pectorale. *Echinochimaera snyderi*, nov. sp., diffère de l'espèce-type par la présence d'une famille dentaire antérieure et supérieure de type successif aussi bien que par des caractères des plaques dentaires et de la première nageoire dorsale. Les nouvelles espèces *E. kellyi*, *E. sulphurea*, *E. indiana* et *E. elusiva* sont décrites à partir de plaques dentaires isolées du Chestérien d'Indiana. La morphologie et le mode de croissance sont comparés avec les chimaeroïdes récents et plusieurs stades ontogénétiques de cochliodontes. Les plaques dentaires du Mississippien ressemblent étroitement à celles de *Echinochimaera*, et sont dérivées par rapport aux plaques dentaires des chimaeroïdes comme des cochliodontes, tandis que les plaques des chimaeroïdes récents proviennent très vraisemblablement d'un stade juvénile d'une plaque dentaire de cochliodonte par pédomorphose. Sur la base des données disponibles, les Echinochimaeroidei sont le groupe-frère des Chimaeroidei, et les Chimaeriformes sont le groupe-frère dérivé des Cochliodontiformes.

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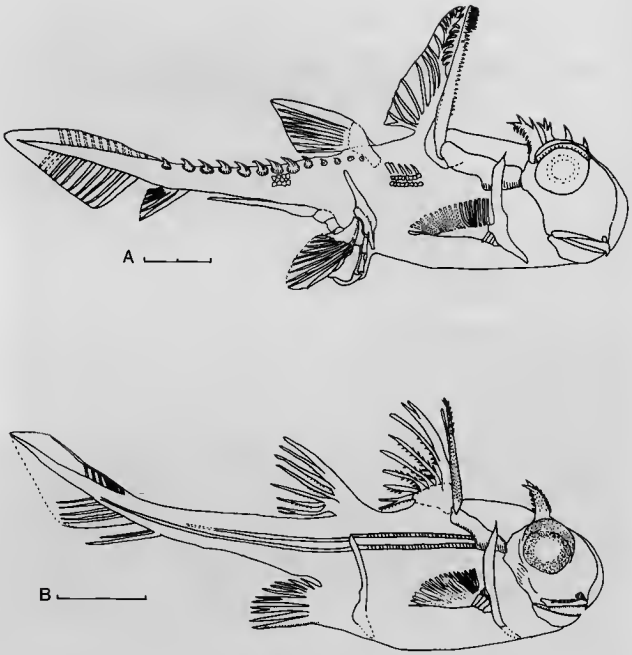


FIG. 1. — A, *Echinochimaera meltoni*, CM 30630, male. B, *E. meltoni*, female, after CM 35526, CM 41028. Scale in cm.

Source : MNHN, Paris

Introduction

The Lower Carboniferous *Echinochimaera meltoni* was described as sharing numerous characters with modern Chimaeriformes, including the presence of prepelvic tenaculae and a dentition of the same tooth plate numbers, relationships and positions (Lund, 1977; 1986). *E. meltoni* differs primitively in having a complete placoid squamation and lacking a frontal clasper, and autapomorphously possessing a second dorsal basal plate supporting the fin, as well as extraordinary male secondary sexual dimorphism.

New material of *E. meltoni*, the discovery of a second species of *Echinochimaera* from the Bear Gulch Limestone, the discovery of several species of chimaeroid jaws from the midcontinental Mississippian of Indiana, and of early growth stages of a Bear Gulch Limestone cochliodont, allows considerable refinement of knowledge of the structure and relationships of the Chimaeriformes.

Abbreviations : American Museum of Natural History, Ichthyology, New York (AMNH); Carnegie Museum of Natural History (CM), Pittsburgh, Pa.; University of Montana Geological Museum (MV), Missoula, Mont.

Material

Subclass **Holocephali**

Order **Chimaeriformes**

Suborder **Echinochimaeroidei**, Lund, 1977

Echinochimaera meltoni Lund, 1977
(Figs. 1-2)

Diagnosis: Lund, 1977.

Remarks: Several morphological features have been clarified through additional specimens. The occipital spine, rather than being median, is a paired structure in both sexes (Fig. 2A). Details of the pectoral fin endoskeleton reveal a structure very close to that of the modern chimaerids, and a restoration of both mature male and female are given in Fig. 1. A lateral view of the jaw plates of a well preserved specimen are illustrated in Fig. 2B.

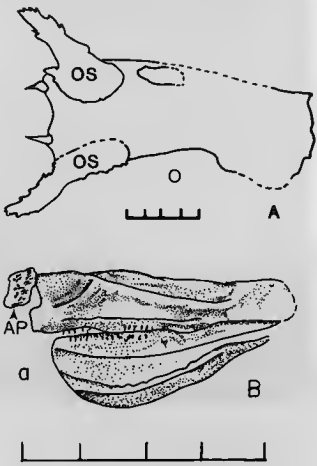


Fig. 2. — A, *Echinochimaera meltoni*, W. Hawes coll. 85-71606, male, dorsal surface of head. B, *E. meltoni*, CM 35526, female, 37 mm snout-vent length, jaws in labial view. Abbreviations: a = anterior; AP = anterior tooth plate; O = orbit; OS = occipital spine.

Echinochimaera snyderi, nov. sp.
(Figs. 3-4)

Type specimen: MV 5373, head and pectoral fin in counterpart.

Referred specimen: CM 37536, complete small specimen in counterpart.

Provenance: Upper Mississippian (Chesterian, Namurian E2b) Bear Gulch Limestone member, Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Source : MNHN, Paris

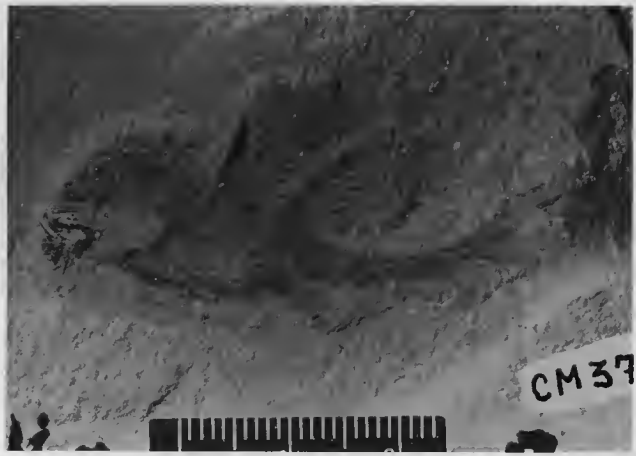


FIG. 3. — *Echinochimaera snyderi*, nov. sp., CM 37536. Scale in mm.

PROVISIONAL DIAGNOSIS: *Echinochimaera* differing from the type species by having: a separate tooth family in the anterior upper tooth position; the labial aspect of the lower jaw plate not narrowing posteriad; the posterior upper plate apparently with both labial and lingual tritoral ridges; a series of horizontal rays present between the first dorsal fin spine and the radials of the body of the fin; and a paired row of enlarged dorsal scales between the cranium and the first dorsal fin as well as posterior to the second dorsal fin.

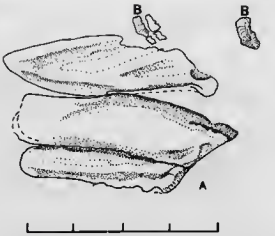
Meristics: First dorsal fin, 14 radials; second dorsal fin 10; pelvic, 9 or 10; anal 6. Measurements in mm (CM 37536): Total length, 59.1; snout-vent length 31.5; head length, 9.7 (MV 5373, 12.9); snout-D1 length, 13.6; snout-D2 length, 20.2; vent-anal length, 12.9; post-anal length, 14.7; postcranial height 11.4; height at pelvic origin 8.5; height at vent, 4.1; height at anal origin, 2.3.

ETYMOLOGY: Named for Bryan Snyder, for many years of friendship and invaluable volunteer assistance in the field.

DESCRIPTION: There is little morphology available to add to that included in the diagnosis. The specimens are small and evidently immature, only traces of calcification of the neurocranium are visible as well as the tall dorsal process of the pelvic girdle.

Both external and internal views of the posterior upper jaw plate are visible (Figs. 4B, C). No traces of tritoral material are visible on the labial surfaces of either specimen. The labial tritoral ridge extends posteriad for less than half of the length of the jaw plate, and there are indications that, unlike *E. meltoni*, *E. snyderi* upper jaw plates possess a lingual tritoral ridge as well.

Source : MNHN, Paris



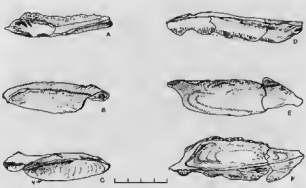


FIG. 5. — *Echinochimaera kellyi*, nov. sp., A-C, CM 44517, holotype lower jaw plate in labial, oral and aboral views, anterior to the right. D-F, CM 44515, upper jaw plate in labial, oral and aboral views, anterior to the left. Scale in mm. Abbreviation: V = vascular vestibule.

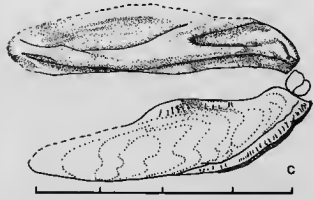


FIG. 4. — *Echinochimaera snyderi*, nov. sp., A, MV 5373, holotype, jaws in labial view. B, MV 5373, holotype, anterior upper tooth. C, CM 37536, upper jaws in labial (above) and lingual (below) views. The aboral surface of the lingual process is represented in impression. Anterior to the right. Scales in mm.

Echinochimaera kellyi, nov. sp.
(Fig. 5)

TYPE SPECIMEN: CM 44517, lower jaw plate.

REFERRED SPECIMENS: CM 44514, anterior parts of 4 upper plates; CM 44515, complete upper plate; CM 44516, complete upper plate, very small; CM 44518, complete lower plate.

PROVENANCE: Indian Springs Shale member of the Big Clifty Formation, Stephensport Group, Chesterian. Intersection of I-64 and state route 35, Sulphur, Crawford County, Indiana.

CHARACTERIZATION: The lower jaw is slim in labial view, gradually tapering to the symphysis, with a prominent posterolateral boss dorsal to a posteriorly facing fossa. The labial lamina is concave posteriorly, with a 180° wraparound of the lateral surface of the jaw. The labial groove lateral to the tritoral ridge is not bordered by a prominent ventral ridge. There is a single narrow labial tritoral ridge and an orally slightly concave lingual platform.

ETYMOLOGY: Named for Dr. Stuart Kelly, who brought this locality to my attention.

REMARKS: The upper jaw plates believed to be associated with the type lower jaw plate are also slim in labial view and bear a single labial tritoral ridge of irregular profile; the lingual platform is anteromesially notched, evidently for reception of the anterior tooth position, as in *Echinochimaera meltoni*. The lingual platform is slightly orally concave.

Tritoral ridges appear to consist of the material called coronal pleromic tissue in gross examination, and give the strong impression on casual examination or on weathered jaw plates of consisting of a series of attached villiform teeth (Lund, 1977, fig. 14). Available material of *Echinochimaera* is insufficient to permit thin-sectioning for analysis.

The posterolateral boss and posterior fossa are presumed to be areas of insertion for the preorbitalis and adductor mandibularis musculature respectively.

Source : MNHN, Paris

Echinochimaera sulphurea, nov. sp.
(Fig. 6)

TYPE SPECIMEN: CM 44519, upper jaw plate.

PROVENANCE: Indian Springs Shale member of the Big Clifty Formation, Stephensport Group, Chesterian. Intersection of I-64 and state route 35, Sulphur, Crawford County, Indiana.

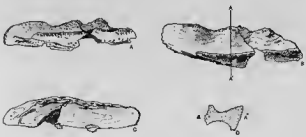


FIG. 6. — *Echinochimaera sulphurea*, nov. sp., CM 44519, holotype. A-D, upper jaw plate in labial, oral, aboral and sectional views. A-A' = line of sectional view. Scale in mm.

CHARACTERIZATION: The palatal plate is very narrow in labial aspect, with the rim of the labial groove not outstanding; the profile of the labial tritor is subdivided into a short anterior " cusp " and a longer posterior ridge, that does not extend to the posterior limit of the plate. Three broad tritoral " cusps " project along the mesial margin of the lingual platform; the anterior margin of the lingual platform is convex antero-mesially.

REMARKS: The external surface of the labial lamina is shiny and ornamented with a series of shallow pits of unknown significance. The lingual tritors are relatively coarse in texture, with tritoral material extending aborally along the entire mesial surface of the plate. This unique specimen is unaccompanied by any lower jaw plate that obviously corresponds to it.

Echinochimaera indiana, nov. sp.
(Fig. 7 A-D)

TYPE SPECIMEN: CM 44520, lower jaw plate.

PROVENANCE: Indian Springs Shale member of the Big Clifty Formation, Stephensport Group, Chesterian. Intersection of I-64 and state route 35, Sulphur, Crawford County, Indiana.

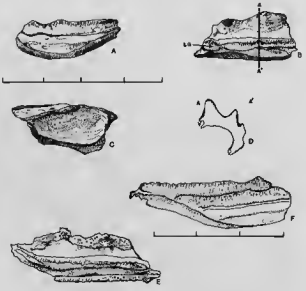


FIG. 7. — A-D, *Echinochimaera indiana*, nov. sp., CM 44520, holotype lower jaw plate in labial, oral, aboral and sectional views. A-A' = line of sectional view. E-F, *E. eluriva*, nov. sp., CM 44521, holotype lower jaw plate in labial, oral views. Scales in mm. Abbreviations: LG = labial groove; V = vascular vestibule.

CHARACTERIZATION: The lower jaw plate is relatively short and anteriorly deep in labial view, and tapers rapidly posteriorly. The labial lamina is shiny and smoothly finished externally, internally concave, and wraps around the lateral surface of the jaw 180°; the ventral margin of the labial lamina bears a smooth, ventrally facing groove; and the labial groove is bordered by an outstanding lower rim. The profile of the labial tritoral ridge is subdivided into a short anterior " cusp ", a slight middle " cusp " and a posterior ridge that extends the length of the plate. Two coarse tritors lay along the mesial area of the lingual platform.

REMARKS: The lower jaw plate of *Echinochimaera indiana* conforms in shape and in details of morphology of the labial lamina and tritor to the lower jaw plate of *E. meltoni*. There are, however, no traces of lingual tritors in any known specimen of *E. meltoni*.

Source : MNHN, Paris

Echinochimaera elusiva, nov. sp.
(Fig. 7 E-F)

TYPE SPECIMEN: CM 44521, lower jaw plate.

REFERRED SPECIMEN: CM 44522, upper jaw plate questionably referred to this species.

PROVENANCE: Indian Springs Shale member of the Big Clifty Formation, Stephensport Group, Chesterian. Intersection of I-64 and state route 35, Sulphur, Crawford County, Indiana.

CHARACTERIZATION: The lower jaw plate is relatively deep in labial aspect and tapers strongly posteriorly. The labial lamina is shiny and smoothly finished externally, and concave internally, with a moderate degree of overlap of the lower jaw. Two sharp tritoral ridges are prominent in labial view, the lateralmost ridge extending farther forward and ending considerably anterior to the more elevated internal ridge. The internal ridge curves mesiad posteriorly, both ridges are cuspidate in profile, and a narrow labial groove with an outstanding rim is seen ventral to the lateralmost ridge. The mesial area of the lingual platform bears a coarse, somewhat subdivided tritoral ridge.

ETYMOLOGY: *Elusiva*, signifying the rarity of isolated chimaeriform tooth plates in the Palaeozoic.

REMARKS: The jaw plate of *Echinochimaera elusiva* is damaged lingually, and the precise shape and extent of the lingual tritor cannot be determined, but it appears to have been subdivided into an anterior and a posterior tritor.

DISCUSSION

The introduction of several species based upon isolated jaw elements is done with great reluctance, but none of these jaws corresponds completely to the jaw elements of either known holomorphic species of *Echinochimaera*. Further, there is no indication, based on the limited available data on variability in the latter genus, that the gross features used in the specific characterizations are subject to major intraspecific variation. The jaws of *E. kellyi* most closely resemble those of *E. meltoni* in oral view, both in shape and in lacking a lingual tritoral row. The *E. indiana* lower jaw is very similar to that of *E. meltoni* in labial view, but bears a lingual tritoral area not present in that species. The jaws of *E. snyderi*, on which a lingual tritoral row has been interpreted, most closely resemble that of *E. sulphurea* in oral view, but do not approach it in labial view.

The jaw plates of echinochimaeroids differ from those of chimaeroids in: the presence of a labial lamina external to a portion of the lateral surface of the fibrocartilage-calcified jaw; in bearing a lingual platform parallel to the same (frontal) plane as the occlusal edge of the labial tritor; and in having minimal lingual growth. The jaw plates are thus positioned on the crests of the jaws, as in ptyctodonts.

Ørvig (1985) discusses four changes that would be necessary in the transition from a tooth plate of cochliodont type to a chimaeroid plate. They are: 1) change of growth from a transverse to a vertical direction relative to the jaw cartilages; 2) disappearance of the compact basal layer; 3) a new hard-tissue framework, compact superficially and on the sides while trabecular internally; 4) transformation of coronal hard tissue to separate, basally evergrowing pleromin columns.

Criterion 1 is actually not a change in growth relationship of plate to jaw but one of plate to occlusal surface; the oral surfaces of cochliodont plates broadly occlude against each other. Jaw plates of *Hydrolagus collei* and *Rhinochimaera pacifica* meet edge to edge at acute angles and lack pleromin tritoral surfaces. In *H. collei*, strings of intratrabecular "compact pleromin" (Ørvig, 1985) tritors are exposed only at the occlusal edges of plates, strengthened by an osteodentine matrix again localized at the occlusal edges (Fig. 8). In *Rhinochimaera pacifica*, where occlusion of the plates is strictly edge to edge, the pleromin nodules are very small and conspicuous tritors are absent (Dean, 1906). The plates of *Callorhynchus* (Fig. 10), *Chimaera phantasma* (Ishiyama *et al.*, 1985) and *Harriota ragleighana* (Ørvig, 1985), where there is plate to plate occlusion, bear tritors of "vascular pleromin" that are exposed by wear. Tooth plate growth relationships are the same in cochliodonts, chimaeroids, echinochimaeroids, and in most elasmobranchs, with new material added to

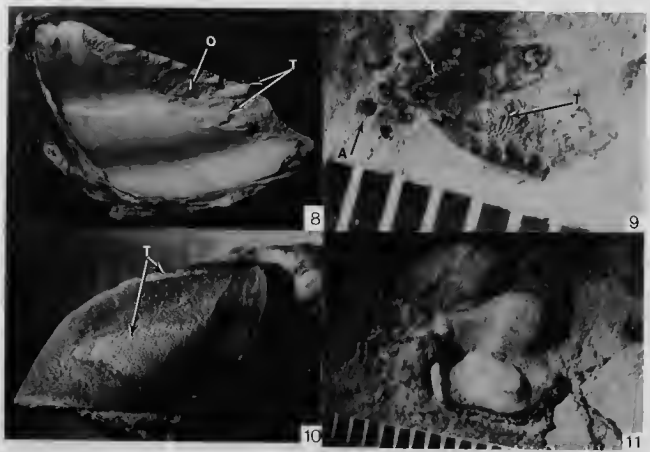
Source : MNHN, Paris

the plate and the plate vascularized at the lingual border. Echinochimaeroid jaws differ in subsequent lingual growth being minimal relative to vertical development of the tritor ridges. This character state can clearly have originated with a paedomorphic tendency in the sense of Bemis (1985); heterochronic mutation is the most reasonable explanation for the lack of continued differentiation of protogerms, and severe negative allometry of jaw development relative to other size parameters would be the most visible expression of this change.

Criterion 2 simply involves a change in orientation of the plates relative to the crests of the jaws. A compact basal layer is clearly present in chimaeroid plates, it lacks vascular openings and lies along the lingual surface of the jaw.

The hard tissue framework of criterion 3 is not new to chimaeroids, but is already present in cochliodont plates (Patterson, 1968).

The transformation of coronal tissues (criterion 4) seems to involve the clearest difference between the groups. Although histology of the plates is outside the scope of this report, several points should be noted in regard to this difference. Ørvig (1985) has made a distinction between compact and vascular pleromin in chimaeroid tooth plates that has a strictly positional basis. Compact pleromin originates intratrabecularly and remains as small nodules, while vascular pleromin, also originating intratrabecularly but close to the surface of the plate, undergoes basal growth and merger of the nodules to form the classical coronal dentine of the tritors. Vascular pleromin, with growth, is organised around parallel denteons, and is microstructurally identical to the coronal



FIGS. 8-11. — FIG. 8 — *Hydrolagus collei*, Adelphi University coll., 450 mm male, mandibular plate. FIG. 9 — " Cochl. ", juvenile, CM 30625B, right mandible. FIG. 10 — *Callorhynchus milii*, AMNH 55719, 846 mm female, mandibular plate. FIG. 11 — " Cochl. ", adult female, CM 35527A, tooth plates. Anterior to the left; scales in mm. Abbreviations: A = anterior teeth; L = lower plate; O = osteodentine; T = tritors; U = upper plates.

Source : MNHN, Paris

dentine of cochliodont plates (Lund, in ms). The mineralogical composition of cochliodont tritoral material is currently under investigation.

A series of ontogenetic stages of one Bear Gulch Limestone cochliodont (" Cochl. ", Lund, 1986) shows a transition from juvenile tooth plate morphology that is extremely similar to that of *Callorhynchus* (Figs. 9, 10) and *Harriota* (Ørvig, 1985, figs. 1, 3), to typical adult cochliodont tooth plate morphology (Fig. 11). Additionally, this species has small, separate anterior teeth with limited tritoral surfaces, as does *Echinochimaera snyderi*. The presence of differentiated larval and adult plate morphologies and histologies in chimaeroids (Dean, 1906) that are essentially identical to that of a cochliodont is further evidence that the two groups share an intimate evolutionary relationship.

Ample evidence exists that the tooth plates of cochliodonts are derived from the transformation of separate tooth protogerms to the continuous production of tooth material by single primordia. This has been demonstrated in *Psephodus* (Traquair, 1885) and *Helodus* (Moy-Thomas, 1939) and has been accepted since it was first proposed by Owen (1867). Zonally deposited tritoral regions separated by superficial bone-like tissue are known both for anterior tooth positions (see below) and for principal plates of *Poecilodus* (McCoy, 1848) and *Metopacanthus* (Patterson, 1965). Small cochliodont plates totally lacking tritoral material, furthermore, are not uncommon in the Mississippian, such as Carnegie Museum field number Lund-841506 from the Lombard Formation of Montana; these tooth plates have generally escaped publication and can be presumed to be the early growth stages of plates that subsequently bore tritoral surfaces of coronal dentine. Labial tritoral ridges extending subparallel to the jaws, grossly as in chimaeroids, are maintained in *Echinochimaera*, as are lingual tritors in certain species. Labial, and lingual, ridges of the same form and position are also found in several cochliodont plates, such as *Deltodus* (Lund, in ms.). Separate tritoral nodules, as seen in larval and some adult chimaeroids (Fig. 8; Dean, 1906), are also present in the anterior tooth plates of the holocephalan Chondrenchelyiformes *Harpagofututor* (virtually identical tritors being present in Myriacanthidae), *Chondrenchelys* and *Solenodus* (Lund, 1982; Patterson, 1965). Finally, the assertion that no bradyodont holocephalan has an oral layer of " pallial " dentine covering the coronal material (Patterson, 1965) is inaccurate; this layer is present between tritors and at the immature edge of modern chimaeroid plates, covering the posterior plates of *Chondrenchelys* (Lund, 1982), and covering the immature edge of certain large cochliodont plates from the Mississippian midcontinental United States.

There are two alternative but not mutually exclusive hypotheses that can explain the evolution of modern chimaeroid plates. First, the limited distribution of tritoral material represents a paedomorphic condition relative to that of the cochliodonts and any other possible sister group in the suppression of coronal dentine as well as in the lack of separation of teeth; the juvenile condition of " Cochl. " corresponding to the adult condition of several Recent chimaeroids. In this light, the tooth plates of *Hydrolagus* and *Rhinochimaera* are further derived states in the suppression of pleromin development. Second, the distribution of tritors among chimaeroids, cochliodonts and Chondrenchelyiformes is as subject to the processes of natural selection as the development and positioning of tooth cusps among the mammals and for precisely the same reasons; the feeding mechanism being one of the principal interfaces between the organism and its environment.

Finally, the process of growth of pleromin, and the histology, is very similar to that of later and recent dipnoans (Kemp, written communication, 1983); Smith (1985) details the process of growth of dipnoan plates and their petrodentine tritoral columns. The mineralogy of the pleromin of *Chimaera phantasma* plates, however, is not hydroxyapatite but whitlockite (Ishiyama *et al.*, 1985). Therefore, while documentation is lacking on details of the histologic transformation, a model for the growth of this peculiar histology exists, and ample morphological evidence can be found to suggest this transformation. Ørvig's criteria overestimate the differences between cochliodont and chimaeroid tooth plates, particularly in light of the more derived morphology of echinochimaeroid plates. It is crucial to note, however, that the echinochimaeroids are not intermediate between chimaeroids and cochliodonts in jaw plate development, but derived relative to either of them in mode of jaw plate growth, the presence of a labial lamina, as well

Source : MNHN, Paris

as in some other morphological characters discussed previously.

Males of several species of cochliodonts from the Bear Gulch Limestone have prepelvic tenaculae as well as other characters of pelvic fin and girdle that are shared only by Chimaeriformes (Lund, 1986). The presence of a suite of autapomorphous chimaeriform-cochliodontiform characters indicates that, based on the available data, the Chimaeriformes are clearly the derived sister group of the Cochliodontiformes. Ptyctodont arthrodires lack any internal pelvic fin, girdle or clasper elements, they share no critical derived pelvic characters in common with any member of the class Chondrichthyes, and can have no close relationship with Chimaeriformes. Nevertheless, the remarkably detailed histologic parallelisms between ptyctodonts, holocephalans and dipnoans detailed by Ørvig (1985) indicate a commonality of underlying development that cannot be easily dismissed.

Conclusion

A second species of *Echinochimaera, E. snyderi*, is described from the Bear Gulch Limestone (Chesterian) of Montana. It differs primitively from the type species in having a separate series of replacement teeth in the anterior upper tooth position, and in the derived condition of having a lingual tritoral ridge. Four species are named from the Chesterian of Indiana from isolated jaw plates. These jaw plates are characterized by a labial lamina that lay external to a portion of the jaw, and a lingual platform perpendicular to the plane of the labial tritoral ridge. One or two additional tritoral areas may be present on the plates. Plates are initially formed with a basolingual vascular supply, but growth of the plates is very limited linguo-labially relative to oral growth.

All criteria for a morphological and ontogenetic transformation series between Cochliodontiformes and Chimaeriformes have been satisfied. Paedomorphosis in plate development as well as natural selection pressures in plate occlusion and tritoral distribution are implicated in the evolution of the group. The labial lamina and limited lingual growth of echinochimaeroids are autapomorphous characters in relation to both Chimaeroidei and Cochliodontiformes. The presence of prepelvic tenaculae in male cochliodonts further emphasizes the close evolutionary relationships between the Chimaeriformes and the Cochliodontiformes and refutes any close relationship with ptyctodont arthrodires.

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Source : MNHN, Paris

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Specialized Dentitions in two Cretaceous Mammals from Patagonia

J. F. BONAPARTE

ABSTRACT

The dentition of the Neocomian eupantothere *Vincelestes* from Patagonia consists of two semi-procumbent incisors, a canine and only five postcanines, each of them with a very different morphology. It represents a very derived form not recorded among the Jurassic-Cretaceous mammals of the northern continents. The second case deals with *Gondwanatherium*, a Campanian mammal from Patagonia with hypsodont molars possessing a flat occlusal surface and open roots. It is concluded that the geographic separation of Gondwana and Laurasia from the end of the Jurassic until the end of the Cretaceous, produced a long biogeographic isolation of both supercontinents resulting in some important differences in the mammalian evolution on each of the supercontinents.

RÉSUMÉ

La denture de l'eupantothère *Vincelestes* du Néocomien de Patagonie consiste en deux incisives semi-proclives, une canine et seulement 5 postcanines, chacune d'elles ayant une morphologie très différente. Ce genre constitue une forme très dérivée, non représentée parmi les Mammifères jurassiques-crétacés des continents septentrionaux. Le second échantillon étudié, *Gondwanatherium*, est un mammifère campanien de Patagonie pourvu de molaires hypsodontes, à surface occlusale plane et à racines ouvertes. L'auteur considère que la séparation géographique du Gondwana et de la Laurasie depuis la fin du Jurassique jusqu'à la fin du Crétacé a produit un isolement biogéographique prolongé des deux supercontinents, d'où sont résultées d'importantes différences dans l'évolution mammalienne de chacun d'eux.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 207-215.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

Several discoveries of Mesozoic mammals made in the Early Cretaceous (Neocomian) and Late Cretaceous (Campanian) of Patagonia demonstrate that in South America existed taxa representing adaptative types of mammals already recognized in the northern continents, together with new and notably different taxa showing dentitions with derived characters not recorded in Laurasia.

The study and interpretation of peculiar adaptative types in several Cretaceous vertebrates from Gondwana (Bonaparte, 1986a), led to the conclusion that a significant process of endemism occurred among the Cretaceous continental vertebrates of the Southern Hemisphere. The vicariant event responsible for this was the geographic separation and the resulting biogeographic isolation of the two supercontinents, Gondwana and Laurasia, from the Late Jurassic (Hallam, 1981; Ziegler, 1984), until the Late Cretaceous (Bonaparte, 1984).

Amongst the Gondwanian groups of vertebrates affected by the vicariant event are recognized families of anurans, chelonians, ophidians, lizards, sauropods, theropods, pterosaurs, birds and mammals (Bonaparte, 1986a). In this paper, two mammals with notably derived characters in their dentition are discussed. One of them is an Eupantotheria from Hauterivian-Barremian beds (Bonaparte, 1986b), while the other is a probable Paratheria (Thomas, 1887) from Campanian beds (Bonaparte, 1986b), both of them from northern Patagonia.

Observations

1. *Early Cretaceous Mammal*

During the 1985 field season significant remains of an Eupantothere were collected. They include most of a lower jaw with the complete dentition (Fig. 1) associated with several postcranial bones. The anatomy of this form, *Vincelestes neuquenianus* Bonaparte (1986b), suggests relationships with the Peramuridae and the Paurodontidae.

The specimen was collected in the upper third of the La Amarga Formation, Neuquén Basin, northwestern Patagonia. The bone-bearing beds are fluvial deposits of a regressive stage of the Pacific. The age, Hauterivian-Barremian, is based on palynological studies by Volkheimer *et al.* (1977), on ostracods by Musacchio (1971), and studies of the regional geology (Leanza & Leanza, 1979; Digregorio & Uliana, 1980).

Incisors.

Only two lower incisors are present in this form. They are semi-procumbent; the mesial one is bigger than the second one. Both are triangular in section, with a thick mesial side, the labial face being convex in both directions, and the distal side thin. Both incisors are very close together.

Canine.

The canine was not in its alveolus. It is rather small and the position of the alveolus suggests it was very close to the incisors.

Postcanines.

Vincelestes bears only five lower postcanines, showing notable morphological differences among them. The PM1 is very small, without traces of occlusion; the PM2 is the biggest of the postcanines, linguo-buccally compressed and tall, with a prominent protoconid. The M1 is smaller than the PM2, with indications of some linguo-buccal compression; the protoconid is the biggest cusp, and the position of paraconid and metaconid make an elongate, narrow trigonid. The M2 is a bit lower than the precedent molar and the trigonid makes a wider triangle; the protoconid is also the biggest cusp but not so much as in that of the M1. The talonid is developed towards the buccal side, with a well defined hypoconid, separated by a depression from the protoconid and metaconid. This M2 is very diagnostic for recognizing the affinities of the genus. The M3 is reduced both in height and in the anteroposterior length of the crown. It shows much wear towards the lingual side, which prevents recognition of the paraconid and metaconid. On the buccal side it is still possible to see the protoconid and, following a distinct depression, the hypoconid, proportionally large.

Derived characters of the lower dentition of *Vincelestes*.

The lower dentition of *Vincelestes* shows several derived characters that are very significant for

Source : MNHN, Paris

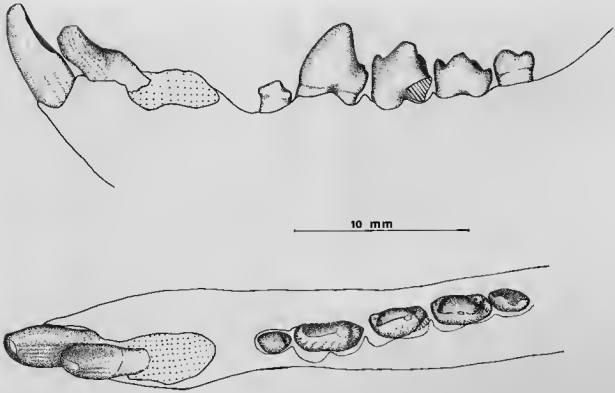

FIG. 1. — *Vincelestes neuquenianus* Bonaparte. Labial and occlusal views of the lower left dentition. The empty alveolus corresponds to the canine. The 5 postcanines represent the complete set of premolars and molars. The specimen is from the Hauterivian-Barremian La Amarga Formation, northeastern Patagonia, Argentina. Collection Museo Argentino de Ciencias Naturales, Buenos Aires, MACN-N 01.

the record of the Eupantotheria (*sensu* Kraus, 1979). The whole lower dentition appears affected by a reduction in the number of elements and by a notable specialization of each of them for a particular diet within the wide range of the insectivorous-carnivorous realm.

The semi-procumbent incisors are only two, of different sizes. The I1 is bigger, thicker and longer, with much wear on the lingual side. The I2 is short and strong, with wear facets on the lingual side. The wear on both incisors resembles that of some Cenozoic carnivores. There is no diastem between the incisors and the canine.

Vincelestes has only two premolars, which show interesting derived characters. The PM1 is very much reduced with no indication of wear facets on its cusps. The PM2 is hypertrophied, transversely compressed, and with the protoconid representing about 90 % or more of the crown volume. The three molars are very different, becoming smaller backwards. The M1 is compressed, with a large protoconid and a rather modest talonid, most of it broken (Fig. 1). The M2 is less compressed, with the protoconid only slightly bigger than the metaconid. The paraconid is well defined as is the talonid, which is oriented on the posteroexternal side of the molar and provided with a hypoconid. The M3 is smaller than the M2, with strong wear of the crown towards the internal side.

Most of these characters of the mandibular dentition of *Vincelestes* are here interpreted as apomorphic characters in comparison with several Eupantotheres, such as *Peramus tenuirostris* (Clemens & Mills, 1971), *Paurodon valens* (Simpson, 1929), *Crusafontia cuencana* Henkel & Krebs (1969), and even with the Aegialodontidae *Kielantherium gobiensis* (Dashzeveg & Kielan-Jaworowska, 1984).

AFFINITIES.

The comparisons made indicate that *Vincelestes* is an eupantothere with affinities to the

Source : MNHN, Paris

families Peramuridae and Paurodontidae, although it possesses derived characters which suggest it represents a different family (Bonaparte, 1986b). The notable reduction in the number of the postcanines, as well as the morphological differences of each of them, appear to be adequately derived characters to distinguish the family Vincelestidae. The degree of development of the talonid and the general distribution of cusps of the M2 appear to suggest some systematic proximity to the Peramuridae and Paurodontidae, in particular with the Peramuridae where the relative position of the talonid towards the buccal side is shared with *Vincelestes*. Also, the relatively narrow and antero-posteriorly elongate molars of *Vincelestes* resemble those of *Peramus*. In the Paurodontidae the talonid is developed towards the lingual side and the molars are proportionally wider.

The notable reduction in the number of postcanines, the morphological differences developed by each of them and the absence of the entoconid (second cusp of the talonid) eliminate the suspicion that *Vincelestes* might be a potential ancestor to *Aegialodon*- or *Kielantherium*-like genera.

This morphologic differentiation of each of the postcanines of *Vincelestes* is, as far as I am aware, unique. I don't know of any Cretaceous mammal from the northern hemisphere bearing only two incisors, two premolars and three molars with so striking differences amongst them as are present in *Vincelestes*. In the case of *Paurodon valens* Marsh, 1887, the number of postcanines is six (Simpson, 1929), and in *Archaeotrigon brevimaxillus* Simpson (1927) it is only five, both forms being from the Late Jurassic of North America. So, the reduced number of postcanines present in *Vincelestes* has antecedents in Late Jurassic species from Laurasia, but this is not the case for the notable differences in the morphology of each tooth of the Patagonian form. The association of derived characters in the number of incisors and postcanines, with the morphologic differentiation of each postcanine of *Vincelestes*, has not been recorded among the Jurassic and Cretaceous mammals of Laurasia.

2. *Late Cretaceous Mammal*

During the fieldwork of 1983, 1984 and 1985, several mammalian teeth were discovered in the Los Alamitos Formation (Franchi & Sepúlveda, 1983), Campanian, of northern Patagonia. The collected specimens include species of Triconodonta, Dryolestoidea, Multituberculata and Paratheria *sensu* Reig (1981) (Bonaparte, 1986b).

The age of this assemblage is based on the Hadrosauridae *Kritosaurus australis* Bonaparte *et al.* (1984), the Titanosauridae gen. et sp. indet. (Powell, 1985), indeterminate remains of theropods and data on the regional geology (Riccardi, 1974; Núñez & Rossi de Garcia, 1981). In Bonaparte (1986b) it is proposed to recognize the Provincial Age Alamitan (Alamitense) based on the characters of the continental vertebrate assemblage recorded in the Los Alamitos Formation.

Among the mammalian teeth discovered are some peculiar molars, with a high crown and open roots, referred to the Paratheria and showing derived characters which merit a special discussion as they are unknown among the Cretaceous mammals.

DESCRIPTION.

Only isolated molars, complete or fragmentary, are available of this Late Cretaceous mammal characterized by hypsodont molars. Some of them have been described as *Gondwanatherium patagonicum* Bonaparte (1986c) whilst others show significant differences that might represent different species or genera of the same group of mammals. Because of the derived characters present in the molars it has not been possible to differentiate between uppers or lowers, nor to determine the relative position in the tooth row. These hypsodont molars have high and prismatic crowns and open roots, with three figures of enamel transversely oriented on the occlusal surface (Fig. 2). The enamel figures, rather complex in design, have different patterns according to the wear of the molars. In the molars with little wear (Fig. 2C, D), each of the enamel figures are small and subcircular. In molars with intense wear such figures occupy most of the transversal length of the occlusal surface, enclosing dentine spaces.

On the occlusal surface there are no normal cusps or other characters of a tritubercular dentition that might help to recognize labial or lingual sides. However, the elevated side of the crown, where three lateral lobules are well

Source : MNHN, Paris

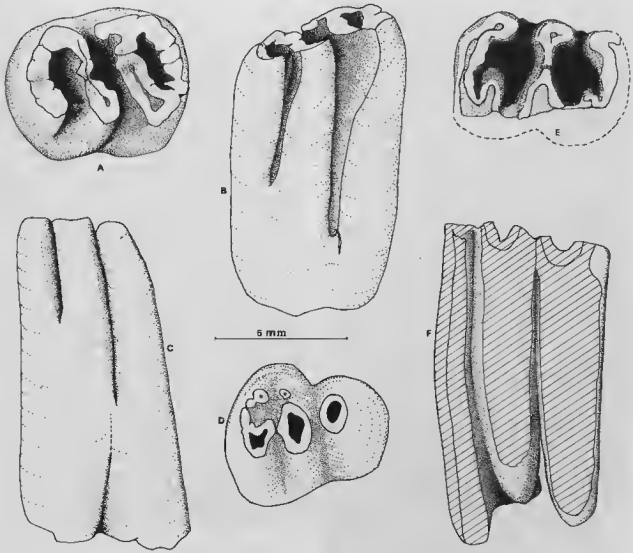

FIG. 2. — *Gondwanatherium patagonicum* Bonaparte. A and B, occlusal and labial views of a referred specimen; C and D, labial and occlusal views of an almost unworn specimen; E and F, a molar (or premolar), anterioposteriorly broken, showing the characters of the cones and the structure of the root region. All these teeth are from the Late Cretaceous (Campanian), Los Alamitos Formation, northeastern Patagonia, Argentina. Collection Museo Argentino de Ciencias Naturales, Buenos Aires, MACN-RN 23; 24 and 25.

developed, is considered here as the labial side. On the lingual side only two lobules are present (Fig. 2).

In the region of the open root the perimetral wall, made of enamel and dentine, is transversely compressed. Inside the opening of the root and at some distance from the border of it, the closed cones of dentine descending from the occlusal surface are visible. These molars are relatively large for the standards of Mesozoic mammals: about 5 mm in diameter of the occlusal surface and 10 mm in height of the crown.

DERIVED CHARACTERS AND AFFINITIES OF THE *GONDWANATHERIUM* MOLARS.

Compared with Late Cretaceous mammals recorded in South America and other parts of the world, such as Triconodonts, Multituberculates, Dryolestoids, Metatherians and Eutherians, these hypsodont molars exhibit several

Source : MNHN, Paris

derived characters of special interest. Among them we recognize: a high crown, prismatic in shape, with one large open root; occlusal surface slightly concave, without normal cusps and with a slight anteroposterior depression as a result of propalinal movements during mastication; three independent figures of enamel and dentine that change shape with wear are transversely placed on the occlusal surface; prolongation towards the root region in the shape of cones of such figures; presence of three wide lobules on the external side of the molars, and of two on the lingual side.

Such a molar of *Gondwanatherium patagonicum* shows several basic characters which resemble the molars of some rodents. However, after detailed comparisons, several important differences are apparent, such as the number and characters of the lobules present on the lingual and labial sides, as well as the peculiar three figures of enamel present in *G. patagonicum*. The general, superficial similarities to the molars of some rodents are interpreted here as the result of convergence of different groups of mammals to a comparable diet, and not to phylogenetic relationships. It is well known that the rodents developed hypsodonty in post-Eocene times. Probably, hypsodont rodents and *Gondwanatherium* correspond to rather comparable adaptative types, at least in the postcanines, developed in very different lineages and epochs.

Scillato Yané & Pascual (1985) described a molar referred to the Xenarthra, *Sudamerica ameghinoi*, Middle Palaeocene of Patagonia, on which the family Sudamericidae was proposed. This molar is hypsodont, with four symmetrical lobules on the lingual and labial sides, and with a strip of enamel all around the perimetral border of the occlusal surface. In addition, three small, subcircular figures of enamel are present in between each of the indentations made by the lobules. The strong differences in the morphology of the lobules and the distribution of the enamel suggest that *Gondwanatherium* and *Sudamerica* correspond to different families (Bonaparte, 1986c). However, the relative temporal and geographic proximity, plus the hypsodonty recorded in these two genera, may be good indications that they belong to the same order or superorder of mammals, and that possibly *Gondwanatherium* may be part of the ancestral group to the Xenarthra.

Discussion

The derived characters of the *Gondwanatherium* molar represent a complex adaptation to herbivorous diets with a high content of siliceous cells. This adaptative type is widely recorded amongst Cenozoic mammals, having independently developed in several orders, such as Pilosa, Cingulata, Rodentia, Lagomorpha, Perissodactyla, Notoungulata, Hyracoidea, Tubulidentata, etc. But only amongst the Xenarthra is it known that hypsodonty was present since the Middle Palaeocene (Scillato Yané & Pascual, 1985), and developed in all the lineages of this superorder. In all the orders except Pilosa, Cingulata and Tubulidentata, hypsodonty occurs only in some of the families that comprise such orders, and generally after the Eocene-Oligocene boundary or even later. In the Equidae, hypsodonty developed only in *Parahippus* and some later forms, at the beginning of the Miocene (Peyer, 1968).

The record of hypsodonty, including that of *Gondwanatherium patagonicum*, suggests that it was achieved at several epochs of the evolutionary history of the mammals, from at least since the Late Cretaceous until the Miocene or perhaps later. It also suggests that the presence of such a dental character represents a synapomorphy for all the lineages of the superorder Xenarthra, which means that their common ancestor was probably a hypsodont form.

Conclusion

At the beginning of this paper I briefly cited the biogeographic isolation of the Gondwana and Laurasia supercontinents as the vicariant event responsible for the Cretaceous endemisms of Gondwana (and of Laurasia). The available evidence suggests that from the Late Jurassic (?Oxfordian, see Hallam, 1983) until the Late Cretaceous (?Campanian, see Bonaparte, 1984), both supercontinents were separated as a result of the opening of the North Atlantic and the union of the Tethys with the Pacific. It means that for about 80 m.y. probably no substantial interchange of terrestrial faunas between both supercontinents occurred. The identity of the

Source : MNHN, Paris

Pangean continental vertebrate faunas recorded since the Late Permian-Early Triassic (Barberena *et al.*, 1985) until the Callovian (Bonaparte, 1979) was progressively lost through the Cretaceous. During the cited interval of about 80 m.y. some limited faunal interchange probably did occur, especially towards the end of the Jurassic (Hallam, 1983) and eventually in the earliest Cretaceous, but it was not enough to prevent the development of a remarkable endemism. Such endemism was apparent in the Neocomian and became very significant from the Aptian onwards. At least in South America the Cretaceous isolation ended in the Campanian (Schmidt-Effing, 1979), when a significant interchange of terrestrial faunas occurred between Central and South America, with the resulting mixture of endemic and allochthonous lineages (Bonaparte, 1984).

The long biogeographic isolation of the two supercontinents would have conditioned the appearance of adaptative types in Gondwana somewhat different from those of Laurasia, not only in the case of the two mammals discussed here, but also amongst the freshwater fishes (Cione, pers. comm.). On a more speculative basis, we interpret that the magnitude of the vicariant event was probably enough to affect not only the vertebrates, but perhaps to a significant degree the Gondwanian Cretaceous biota.

The dentition of the Cretaceous mammals here discussed within the general hypothesis of biogeographic isolation, offers several perspectives for its evaluation and interpretation. We note the following:

1) The Neocomian and Late Cretaceous mammals of South America show that the evolution of this group of vertebrates did operate through the whole Cretaceous on this continent and, by extension, possibly on the whole of Gondwana. Consequently what is known of the evolution of the Cretaceous mammals from Laurasia may be only a part of the whole history.

2) In South America, and probably in Gondwana, there developed from ancestors of Pangean distribution, adaptative types similar to those in Laurasia (Triconodontidae, Multituberculata, Dryolestidae), along with distinctive types with notable derived characters in their dentition, not recorded in Laurasia (Vincelestidae, Gondwanatheriidae, Mesungulatidae).

3) The specialized dentition of the Neocomian *Vincelestes* from Patagonia, adapted to an insectivorous-carnivorous diet, has no parallel among the Cretaceous Theria of Laurasia.

4) The notable hypsodonty of the Campanian *Gondwanatherium* from Patagonia demonstrates that this adaptive character was developed in South America, and possibly in Gondwana, much earlier than among the Laurasian mammals.

5) The presence of hypsodonty in every lineage of the superorder Xenarthra recorded in South America since the Middle Palaeocene, suggests they inherited this derived character from Cretaceous ancestors of the *Gondwanatherium* type.

6) The development in the Cretaceous of Patagonia, and probably Gondwana, of mammalian lineages with notable derived characters in the dentition suggests that the Cretaceous biota of this supercontinent had characters and components somewhat different from those of Laurasia. Such differences would have generated particular adaptive types among the mammals and other groups of vertebrates. However, they were possibly limited and did not obscure a general identity.

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Source : MNHN, Paris

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Dentition and Ways of Life in Cenozoic South American Rodent-Like Marsupials. Outstanding Examples of Convergence

R. PASCUAL, A. A. CARLINI & L. J. M. DE SANTIS

ABSTRACT

The most rodent-like Soutb American marsupial and a truly placental rodent of the same age (Colbuehuapian, Late Oligocene-Early Miocene?) and locality (Gaiman, Chubut, Patagonia) show similar dental features that are bere interpreted as convergent adaptations to close ecological niches. The evidence at band indicates tbat tbe marsupial and placental rodent dental similarities result from similar morpbogenetic pathways. Furtbermore, the late Tertiary-Pleistocene record sbows that a quite similar convergence process was repeated by distinct marsupials (Argyrolagidae) and caviomorpb rodents (Octodontidae).

RÉSUMÉ

Le marsupial sud-américain le plus semblable á un rongeur, et un vrai rongeur placentaire de même âge (Colhuehuapien, fin de l'Oligocène-début du Miocène ?) et de la même localité (Gaiman, Chubut, Patagonie) présentent des caractères dentaires semblables qui sont interprétés ici comme une adaptation convergente à des niches écologiques voisines. Les données disponibles indiquent que les similitudes dentaires du marsupial et du rongeur placentaire résultent de parcours morphogénétiques comparables. En outre, les fossiles du Tertiaire tardif-Pleistocène montrent qu'un processus de convergence très voisin fut répété cbez d'autres marsupiaux (Argyrolagidae) et des rongeurs caviomorpbes (Octodontidae).

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Source : MNHN, Paris

Introduction

It is well known that living and extinct South American marsupials underwent an adaptive radiation that led them into many ways of life similarly occupied by placentals on the northern continents and Africa. Among the extinct marsupials so far known the inference of their ways of life has mainly been accomplished by means of dental morphology and the arrangement of the different elements within the tooth series. A detailed analysis of one of these examples of convergence, in the omnivorous-carnivorous ecological zone, was made by Marshall (1977, 1978).

In South America different cases of marsupial-placental convergences toward the same adaptive zone were either synchronous or diachronous. The synchronous ones were always between South American marsupials and extra-South American placentals, e.g. Bonapartheriidae vs. Carpolestidae primates (see Pascual, 1980), or Proborhyaeninae borhyaenids vs. some Creodonta (see Bond & Pascual, 1983). Among the diachronous examples there are two main types: (a) early South American marsupials and later placental immigrants, e.g. Borhyaenoids vs. placental carnivores; and (b) South American specialized marsupials and extra-South American specialized placentals, e.g. Thylacosmilidae vs. some Nimravidae. These examples appear to support the idea that extinction of the most specialized South American marsupials was the result of active competition with immigrant placental counterparts (Patterson & Pascual, 1972; Marshall, 1977, 1978). Thus it has been thought that the evolution of truly rodent-like marsupials was only incipient because placental rodents reached South America fairly early in history (Simpson, 1980: 64). This inference has been further supported by the fossil record of the continent: heretofore no coetaneous marsupial and placental pair of " ecological counterparts " had been recorded. Now, we offer an unexpected example of a pair of " ecological counterparts ", a marsupial and a placental, not only coetaneous but apparently sympatric. They are the only " truly " rodent-like marsupial and placental rodent hitherto known, both recorded in the same late Oligocene (Colhuehuapian) site and level. Furthermore, apparently they both represent end products of specialized mammals, such as those fossorial terminal-fossil and living Octodontidae rodents presently inhabiting the drier and arid regions of southern South America.

Synthetically we also analyze two other extinct rodent-like South American marsupials with two main purposes: (1) to show that the Colhuehuapian convergent occurrence was differently iterated (*sensu* Simpson, 1961) during the late Miocene-early Pleistocene by systematically distinct marsupials and rodents; and (2) to show that both groups and events followed quite similar dental morphogenetic trends. Each of the two occurrences is analyzed as linked to comparable changes in physical environments owing to diastrophic events and to apparently related global climatic changes.

Observations

The Colhuehuapian marsupial and placental pair of " ecological counterparts " was recently studied, both being known by fragmentary mandibles with almost the whole dentition. The first (Figs. 1A, B; 2A, B, C), as the marsupial the most distinctly convergent to some caviomorph fossorial rodents, was regarded as a distinct clade of South American marsupials, representing the type of a new family, and assigned to a new superfamily (Pascual & Carlini, in press). The second, named *Cephalomyopsis hypselodontus* (Vucetich, 1985) (Figs. 1C, D; 3J), is the most advanced Cephalomyidae rodent (along with the Miocene *Cephalomys*?, n. sp. *fide* Frailey, 1980), with euhypsodont (*sensu* Mones, 1979) and octodontoid cheek teeth such as those characterizing the later eremic and fossorial Octodontidae.

Both the marsupial and the rodent were recovered from Colhuehuapian mammal-bearing beds (latest Oligocene -early Miocene) (see MacFadden *et al.*, 1985) exposed in the Gaiman region of Patagonia (Chubut province, Argentina). From an ecological point of view, it is suggestive that this mammal-bearing level was recognized as composed of soft steel-gray, fine, cross-bedded sandstone, and stratigraphically overlain by thick-bedded, pale, yellowish tuff, with marine pelecypods, and remains of sharks, rays, cetaceans, and penguins. According to Simpson (1935: 17), very probably this terrestrial mammal-bearing level consisted of unconsoli-

Source : MNHN, Paris

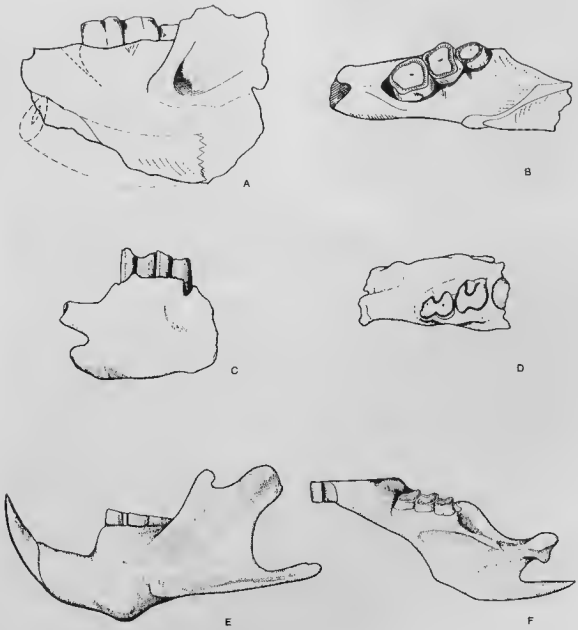

FIG. 1. — Colhuehuapian marsupial (gen. et sp. nov.). Fragment of a left mandibular ramus, with the only three cheek teeth : *A*, labial view; *B*, occlusal view.
Cephalomyopsis hypselodontus Vucetich. Fragment of a left mandibular ramus: *C*, labial view; *D*, occlusal view.
Ctenomys sp. Left mandibular ramus: *E*, labial view; *F*, occlusal view.
(Not to scale).

Source : MNHN, Paris

dated sediments present when the sea advanced. To us it has the general appearance of remnant dunes, very probably marine dunes.

Compared to the most fossorial caviomorph rodents presently known, such as the Octodontinae and Ctenomyinae octodontids, the Colhuehuapian *Cephalomyopsis* cephalomyid and the rodent-like marsupial show the following main mandibular and dental convergent features (Fig. 1).

MANDIBLE.

1. Short and deep.
2. Symphysis subvertical and unfused.
3. Masseteric fossa well developed.
4. Coronoid process forming a strong and salient lamina, bordering posterolaterally a conspicuous retromolar basin.
5. Pre-cheek teeth diastema.

TEETH.

6. Rodent-like gnawing incisor, open-rooted, elongated and with curved extra-alveolar portion.
7. Intra-alveolar portion of incisor lengthily extended within the mandibular ramus.
8. Posterior intra-alveolar portion of incisor forming a remarkable lingual prominence.
9. Reduced number of simple prismatic cheek teeth permanently open-rooted (euhypsodont), forming a closed molariform series.
10. Occlusal facets practically flat, although dentine forms a shallow basin surrounded by the highest enamel layer.
11. Occlusal facets with a slightly deeper anteriolabial-posterolingual wear groove.

Of course, all of these are general shared-derived features, which naturally have the follow-

Octodontidae	*Cephalomyopsis hypselodontus*	*Colhuehuapian rodent-like marsupial*
1. Yes, but within the most specialized cave-dwelling forms, e.g. *Ctenomys*	Yes, but not so much as in *Ctenomys*	Yes, increasing abruptly toward the last molar
2. Yes, but as in 1	Yes	Yes
3. Yes, but shallower and more extended	Unknown	Yes, but dorsal and deeper
4. Yes, but with the retromolar basin relatively deeper and sub-circular	Unknown	Yes, but with the retromolar basin forming a diagonal and straight channel
5. Yes, lower than the cheek teeth alveolar level	Idem Octodontidae	Yes, but reduced because there exists a canine, and to cheek teeth alveolar level (as in primitive rodents, e.g. Paramyidae, Ischyromyidae)
6. Yes	Yes	Yes. Although the enamel surrounds the entire tooth, there is a heavier band along the ventral face
7. Yes, but strongly curved up to below the condyle	Unknown	Yes, but almost horizontal and extended along the ventral border up to below the last molar
8. Yes and widely separated from ascending ramus, i.e. hystricognathous	Unknown, but surely as in the rest of the hystricognathous caviomorphs	Yes, but horizontal and enveloped by the inflected ventral border up to below the last molar
9. Yes, four cheek teeth octodontoid to kidney-shaped in section (Ctenomyinae)	Yes, also four and octodontoid in section	Yes, but only three and square-shaped, with only vanished octodontoid section
10. Yes	Yes	Yes
11. Yes	Yes	Yes

Source : MNHN, Paris

ing various nuances in each of the convergent examples (Fig. 1):

Discussion

A. Morphofunctional analysis

Using as a standard a plesiomorphous marsupial such as *Didelphis marsupialis* (*fide* Hiiemae & Jenkins, 1959), and according to the mandibular osteological features preserved in the new Colhuehuapian rodent-like marsupial, the main masticatory muscles that can be inferred as particularly active are listed below. The homologous muscles developed in such fossorial caviomorph rodents as the Octodontidae are indicated in Fig. 2.

— The development of the masseteric fossa and the coronoid process suggests a well developed external adductor. This is homologous — at least partially — with the lateral masseter, and apparently also with the medial masseter in Octodontidae (see Woods, 1972) (Figs. 2A, 2D).

— The well developed ventral border of the masseteric fossa, as well as of the particularly inflected ventral border (very surely affecting also the angular portion) suggest an expanded and reflected superficial masseter. This is homologous with the superficial masseter in the Octodontidae (see Woods, op. cit.) (Figs. 2A, D).

— The particularly well developed retromolar valley, extended along the coronoid medial face, suggests a prominent internal adductor. This is homologous with the temporal (orbital) in the Octodontidae (Figs. 2B, C, E, F).

— The very well developed macropodid-like pterygoid fossa indicates that there was a prominent internal pterygoid. This is homologous with the likewise prominent internal pterygoid in the Octodontidae (Figs. 2C, F).

According to the function attributed to those muscles in *Didelphis virginiana* by Hiiemae & Jenkins (op. cit.), the following masticatory movements in the Colhluehuapian rodent-like marsupial appear to have been well emphasized:

— Adduction s.s. (crushing): internal and external adductor.

— Retraction: posterior adductor (?) and partially the external adductor.

— Protraction: both superficial masseters, acting in concertation with the internal pterygoid.

— Antero-labial movements: internal pterygoid of one side acting in concertation with the contralateral superficial masseter.

— Postero-lingual movements: adductor complex of one side alternatively acting with the other side.

Summing up, the Colhuehuapian rodent-like marsupial, like the sympatric *Cephalomyopsis* placental rodent and the modern fossorial Octodontidae, achieved a main propalinal movement in concertation with a secondary lateral one (grinding). These movements were assisted by a secondary vertical (orthal) one (crushing).

B. Paleoecology

It is true that an ecological niche cannot be defined only by the organisms living in it, nor by the external world deprived of organisms (Lewontin, 1984). Nevertheless, the masticatory apparatus of the Colhuehuapian pair of ecological counterparts and the extinct and living Octodontidae rodents is so similar that it induces the following inference: it constitutes a common device to accomplish a similar specific function. That is to say, that there have been similar "solutions" to similar "problems". In other words, all of these animals occupied similar ecological niches. Thus, we must agree that the Colhuehuapian marsupial and rodent pair of ecological counterparts inhabited a biotope similar to the ones presently occupied by the octodontid rodents, either within arid to desertic regions with loose sandy soils, or in restricted xeric patches having that kind of loose soils, but within well-watered regions. Of the two living Octodontidae groups, the Octodontinae and Ctenomyinae, the latter is the only one which has species occupying the two above-mentioned biotopes: marine dunes, sometimes within well-watered regions as the "humid pampas", and humid forested environments to predominantly arid to desertic inlands, including even such highlands as the "puna plateau" (see Cabrera & Yepes, 1960). It is evident that the main requirement is a loose sandy soil more than the general regional climatic conditions. The first

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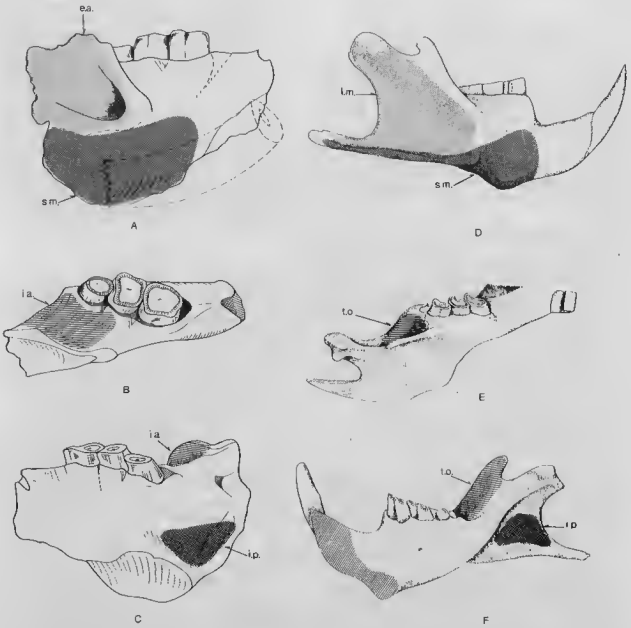

FIG. 2. — Colhuehuapian marsupial (gen. et sp. nov.) (the same as Figure 1, but reversed): *A*, labial view; *B*, occlusal view; *C*, lingual view.

Ctenomys sp. Right mandibular ramus: *D*, labial view; *E*, occlusal view; *F*, lingual view.

Both show the main insertion areas of the homologous masticatory muscles. e.a. = external adductor; i.a. = internal adductor; i.p. = internal pterygoid; l.m. = lateral masseter; s.m. = superficial masseter; t.o. = temporal (*pars orbitalis*). (Not to scale).

Source : MNHN, Paris

biotope conforms better to the lithological evidence: the Colhuehuapian Patagonian mammal-bearing beds are composed of sandy eolian sediments intercalated between typical consolidated Colhuehuapian mammal-bearing tuffites below and marine sediments (Gaiman Formation) above (Simpson, 1935; Pascual & Carlini, 1987). Thus, the lithological as well as the stratigraphical evidence characterize these sediments as continental nearshore deposits, very surely marine dunes. This conclusion is further supported by another peculiar marsupial found in the same locality and level: a true forerunner of the otherwise Miocene-Pleistocene saltatorial Argyrolagidae (being studied by two of the authors, R.P. & A.A.C.). The main features that distinguish these peculiar South American marsupials (Simpson, 1970a, 1970b; Wolff, 1984; and Fig. 3L, M) are already present in this new taxon, but with a complete marsupial cheek tooth number. Very surely this new taxon, like *Argyrolagus scagliai* (Simpson, 1970a, fig. 18) and probably also like the older Deseadan *Proargyrolagus bolivianus* Wolff, 1984 (Fig. 3L), were bipedal-ricochetal and, like all living animals of this general type, adapted to semiarid to arid biotopes, either in desertic areas or in areas of greater rainfall and more vegetation, specially grasslands.

As far as we know, among the Cenozoic South American mammal communities, this is the first record of a habitat divided up into two specific but otherwise similar ecological niches, and respectively occupied by a marsupial and a placental. Among the frequent examples of convergence toward eutherian mammals offered by the South American marsupials (Marshall, 1977), till now this is the only one that succeeded coetaneously and within the same biogeographical range. This is an outstanding and unique example showing that under appropriate historical circumstances the traditional " inferior " and native marsupials were able to share with the " superior " and immigrant placentals even some specific niches. Ecologically there is always a multidimensional niche space. Actually, according to the record and the historical events, the rodent-like marsupial appears to have been occupying such a specific ecological niche well in advance of the Cephalomyidae rodent, and very probably even well in advance of the arrival of the immigrant rodents.

C. *Evolution: Convergence and Iteration*

Not infrequently it happens that different evolving populations or lineages independently go through similar trends. Usually these trends are particularly similar if the lineages in question are more or less closely related. So it is that related lineages splitting off from a common ancestry at about the same time may show similar and simultaneous trends. This phenomenon has been called " parallel trends " or "programme evolution " (Simpson, 1953). On the other hand, unrelated lineages splitting off from quite different ancestries may also show similar trends. This phenomenon has been called convergence, or convergent evolution.

Different South American marsupials converged toward the same adaptive zone occupied by placentals. The most conspicuous examples were mentioned above. But so far as we know, within the South American territory, this phenomenon has not yet been recorded as occurring at the same time, and the final evolutionary products of which had the same biogeographical range, very surely being sympatric. The case of the Colhuehuapian rodent-like marsupial and the *Cephalomyopsis* rodent represents the first of such an example known to date.

There are cogent reasons to admit that the dental features of each member of the pair of " ecological counterparts " were terminal and extreme specializations, departing from a more primitive condition already shared by each ancestor. The successive elongation of the incisor concomitantly evolved with progressive hypsodontism of the cheek teeth. We have not recorded the original steps of both Colhuehuapian marsupial and cephalomyid rodent lineages, but their eight-shaped cheek teeth section (the only remnant feature in the marsupial; Fig. 3N) necessarily had to pass through such a primitive character state as that clearly exemplified by the oldest marsupial *Groeberia* (Patterson, 1952; Simpson, 1970c and Fig. 3K) and the rodent *Platypittamys* (Wood. 1949; Wood & Patterson, 1959; and Fig. 3A). In this respect, the Miocene-Pliocene Octodontidae's dental trend offer an eloquent example (Pascual, Pisano & Ortega, 1965; and Fig. 3B, G, H).

The Oligocene-early Miocene Cephalomyidae and the partially coetaneous and later (Miocene-Present) Octodontidae rodents offer an unique

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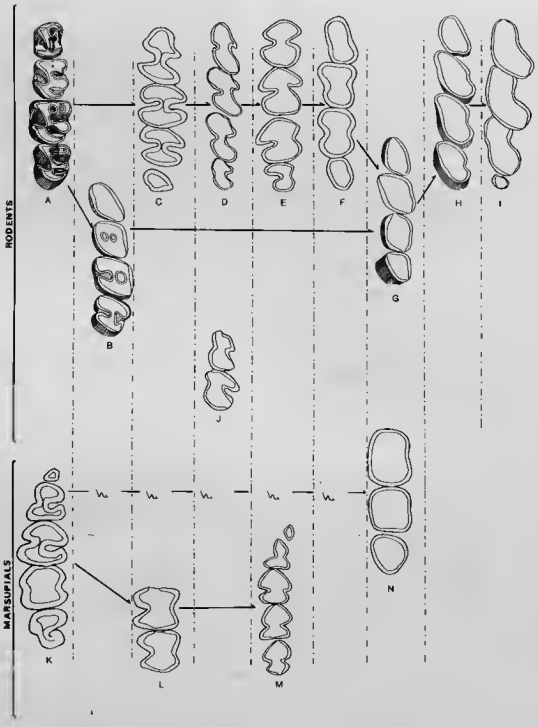

FIG. 3. — Occlusal view or crown section of lower left cheek teeth series (partial or whole).
A, Platypittamys sp.; *B, Phtoramys* sp.; *C, Octomys* sp.; *D, Octodon* sp.; *E, Spalacopus* sp.; *F, Octodontomys* sp.; *G, Palaeoctodon* sp.; *H, Xenodontomys* sp.; *I, Ctenomys* sp.; *J, Cephalomyopsis* sp.; *K, Groeberia* sp.; *L, Proargyrolagus* sp.; *M, Argyrolagus* sp.; N, Colhuehuapian marsupial (gen. et sp. nov.).
Note: Arrows indicate morphogenetical not phylogenetical sequences. Vertical lanes include taxa with similar states of cheek teeth morphologies.
(Not to scale).

Source : MNHN, Paris

example of ecologically similar lineages that arose successively, one after the other. This is another outstanding South American example of what has been known as " successive trends " or " iteration " (Simpson, 1953: 127-131; Pascual *et al.*, 1985: 233-235). On the other hand, the Colhuehuapian (unpublished) to early Pleistocene Argyrolagidae marsupials offer another example of a similar lineage that likewise succeeded the terminal rodent-like marsupial lineage represented by the Deseadan *Proargyrolagus* (Figs. 3L and 3M; see also Wolff, op. cit.; Pascual & Carlini, 1987). So, once again, we have a convergent case of a rodent-like marsupial and a placental rodent, although this time the two forms are not so closely alike. Notwithstanding, these different rodent-like marsupial (Argyrolagidae) and placental rodent (Octodontidae) counterparts followed a quite similar morphogenetical trend of the cheek teeth, and curiously through steps similar to those of the Colhuehuapian marsupial (Fig. 3N) and rodent (Fig. 3J) counterparts, i.e. figure eight-shaped, quadrangular, to finally " semilunar ", (Fig. 3I).

Each of the Colhuehuapian and Miocene-Pleistocene marsupial-rodent convergences appear as evolutionary adaptational phenomena related to repeated environmental changes owing to global desiccation. Geological as well as paleontological evidence points to regarding as steppes or semiarid pampas the environments where the Argyrolagidae dwelt (Simpson, 1970a). Global diastrophic movements in the Late Eocene and Pliocene-Pleistocene are thought to be responsible for, or concomitantly related to, the repeated environmental changes (Pascual, 1984a, 1984b; Pascual & Carlini, 1987), and through them for the origin as well as the extinction of those marsupial and rodent (only the Cephalomyidae) counterparts.

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Dental Evolution in the Endemic Glirids of the Western Mediterranean Islands

J. AGUSTÍ

ABSTRACT

In this paper dental evolution in a number of endemic genera developed in the islands of the Western Mediterranean is examined. The islands are Ibiza, Majorca, Minorca, Sardinia, Sicily, Malta and Gargano. The genera reviewed are *Eivissia, Hypnomys, Tyrrhenoglis, Maltamys, Leithia, Muscardinus* and *Glis*. The evolutionary pattern fits well into a punctuated equilibria model. Two phases are distinguished, the former involving a very rapid evolution towards increasing size, the latter being much slower and involving morphological changes (extra ridges, isolated centrolophs, more robust lophs, molarization of premolars). These changes are the result of local adaptations to dry conditions.

RÉSUMÉ

Dans cet article est examinée l'évolution dentaire de plusieurs genres endémiques des îles de la Méditerranée occidentale. Ces îles sont Ibiza, Majorque, Minorque, la Sardaigne et la Sicile, Malte et Gargano. Les genres passés en revue sont *Eivissia, Hypnomys, Tyrrhenoglis, Maltamys, Leithia, Muscardinus* et *Glis*. Le schéma évolutif s'accorde bien avec un modèle d'équilibres ponctués. Deux phases sont distinguées, la première impliquant une évolution très rapide vers un accroissement de taille, la seconde étant beaucoup plus lente et impliquant des changements morpbologiques (crêtes supplémentaires, centrolophes isolés, lophes plus robustes, molarisation des prémolaires). Ces changements sont le résultat d'adaptations locales à des conditions de sécheresse.

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Introduction

The evolution of the endemic glirids which developed in the Western Mediterranean islands has been the subject of a number of papers. The proposed mode of evolution of these forms in insularity conditions is very characteristic and clearly fits into a punctuated equilibria model (Mein, 1983). Thus, after the settlement of the island, the rodent species undergo a very quick evolution, followed by a prolonged stasis phase. The complicated tectonics in the Mediterranean basin during the Neogene led to the appearance of a number of endemic glirids and an abundant literature exists on their development. In this paper, an attempt is made to test the above mentioned model on the basis of the analysis of its dental evolution. In trying to test the model referred to, two conditions are unavoidable. Firstly, we must know the continental ancestor of the insular species with rough approximation. Secondly, the corresponding age of the fauna is also a necessary datum. Without these data, the evaluation of any morphological or metric change is impossible.

Observations

A. *Review of insular faunas in the Western Mediterranean*

Majorca.

Two different phases of insularity have been detected on this island. The former, represented by the localities of Sta. Margarida and St. Llorenç, displays three different glirid species (*Margaritamys lulli, Carbomus sacaresi* and *Peridyromys ordinasi*) and one lagomorph (*Gymnesicolagus gelaberti*, see Mein & Adrover, 1982 and Adrover *et al.*, 1985). Both *Margaritamys* and *Carbomys* seem to descend from the species *Pseudodryomys ibericus*, perhaps at different times. The age of this fauna has been evaluated in the locality of Sta. Margarida, whose layers were deposited over marine Langhian levels. The origin of the isolation process is probably related to the shift of the Balearic arch to the east and the opening of the Balearic Basin.

A second insularity phase is represented by the classical endemic fauna with *Myotragus* (a caprid), *Hypnomys* (glirid) and *Nesiotites* (soricid), already described by Bate (1909). In Cova Canet, a cave deposit with *Myotragus kopperi* Moya & Pons and *Hypnomys waldreni* Reumer, the paleomagnetic record indicates an Upper Pliocene age (Kopper, 1975). Nevertheless, there exist older deposits in Majorca (with less evolved *Myotragus*), possibly indicating a Lower Pliocene age. The settlement of Majorca by the *Myotragus*/*Hypnomys*/*Nesiotites* ancestors was probably not caused by tectonic features, like the first isolation phase, but was linked to the desiccation of the basin during the Messinian (Moya-Sola *et al.*, 1984). *Hypnomys* is considered to evolve from *Eliomys intermedius* Friant.

Minorca

Two distinct insularity phases can also be distinguished on this island. The former corresponds to the fauna from the Cala Es Pou fissure filling. This deposit was developed over a Messinian reef-stone, itself covered over by marine layers also of Messinian age. The fauna of this phase is composed of a glirid (*Muscardinus cyclopaeus*), a lagomorph (*Trischizolagus* sp. A) and *Geochelone gymnesica* (a giant testudinid). *Muscardinus cyclopaeus* Agustí, Moya & Pons shows greatest affinities with *M. vireti* Mein & Hugueney from the Upper Miocene of Lissieu (MN 13).

After this first Messinian phase, a second one presents the same elements as the *Myotragus* phase of Majorca. The relationships of *Hypnomys* have been discussed in the previous paragraph.

Ibiza.

A first settlement on the island is represented by the fauna from Ses Fontanelles, which presents *Protatera* sp., *Eliomys* sp., *Trischizolagus* sp. B, Insectivora indet., aff. *Thyrrenotragus* sp. and Caprinae indet. The presence of African immigrants (*Protatera*) strongly suggests a Messinian age for this fauna.

A second insularity phase is represented by the fauna from Ca Na Reia, with two glirid species (*Eivissia canarreiensis* Alcover & Agustí and *Hypnomys* sp.), one Caprinae, Chiroptera and *Testudo. E. canarreiensis* is a clear descendant of

Source : MNHN, Paris

Eliomys (probably, *E. intermedius*). *Hypnomys* sp. displays a larger size than any of the known *Hypnomys* species. The Caprinae from Ca Na Reia could be related to the *Myotragus-Nesogoral* group (Moya-Sola *et al.*, 1984). As in the *Myotragus/Hypnomys* faunas, a late Messinian age has been proposed for the origin of the settlement.

Sardinia.

As in the case of Majorca, two very different phases of isolation took place on this island. The former presents a very peculiar association with ctenodactilids (*Sardomys dawsonae, Sardomys antoniettae, Pireddamys ravi*), glirids (*Myomimus* sp., *Microdyromys* aff. *koegniswaldi, Glis major*), insectivores (*Geotrytpus oschiriensis, Nuragha schreuderae, Crocidosorex antiquus*). Some elements of this association indicate a Lower Miocene age. Nevertheless, the absence of most of the typical elements of this period (like the cricetids) is surprising. This fact and the gigantism of *Glis major* strongly suggests that Sardinia was already an island. Another surprising datum is the presence of African rodents (ctenodactilids; De Bruijn & Rumke, 1974).

Several karstified fissures indicate the existence of a second insularity phase, with a more diversified fauna than the other islands in the Western Mediterranean (probably, because of Sardinia's larger size). The oldest deposit, hitherto, (Capo Mannu, Peccorini *et al.*, 1974) presents *Tyrrhenoglis* aff. *figarensis, Apodemus mannu, Rhagapodemus hautimagnensis, Prolagus figaro*, erinaceid indet., talpid indet., cf. *Sus minor*, Caprinae indet. The *Eliomys* affinities of the genus *Tyrrhenoglis* Engesser have been established by Zammit Maempel & de Bruijn (1982).

Malta and Sicily.

In this case, we also have two phases of settlement. The first one, represented by the Sicilian locality of Monte Pellegrino (Thaler, 1972), is probably related to the Messinian event, because of the presence of an African immigrant (the ctenodactilid *Pellegrinia panormensis*), together with that of a glirid (*Maltamys* cf. *göllcheri* de Bruijn), an endemic murid (*Apodemus maximus* Thaler) and a lagomorph (*Hypolagus* sp.). The genus *Maltamys* appears in many other localities in Malta. A second evolutionary stage, *M. wiedincitensis*, displays more derived characters than the previous species. In Malta, *Leithia*, a second glirid genus of larger size but with a single pattern, coexists with *Maltamys* in some localities. The affinities of *Leithia* are not clear (Zammit Maempel & de Bruijn, 1982) but a derivation from *Eliomys* is the most probable hypothesis.

Gargano.

The Gargano karstified complex contains a number of fissure fillings which have yielded a very interesting faunal assemblage (Freudenthal, 1976, 1985; de Giuli *et al.*, 1985). Among the mammals, the most characteristic elements are a giant erinaceid (*Deinogalerix*), an "aberrant" ruminant (*Hoplitomeryx*), a lophodontic arvicolid-like murid (*Microtia*) and an endemic Cricetidae (*Hattomys*). In addition, the glirids are also represented in many localities (genus *Stertomys* Daams & Freudenthal, 1985).

The age and origin of this fauna is a matter of discussion, but it is our belief that some elements permit a certain approximation. Thus, one of the most abundant elements, the murid *Microtia*, shows a superficial similarity with *Stephanomys*. Nevertheless, the pattern of the Upper M1 and the presence of tma * in the Lower M1 strongly suggests a derivation from *Parapodemus* (the presence of a t_6-t_9 ** connection excludes a derivation from *Progonomys*; the absence of t_7 excludes a derivation from *Apodemus*). Moreover, *Hattomys* shows strong *Kowalskia* affinities, with its long mesolophs in the Upper M1, its double protoloph in M1/ and M2/ and the joining of the anterolophid to the labial spur of the anteroconid. The shape of the cusps is also more *Kowalskia*-like than *Cricetulodon*-like. All these data suggest an Early or, at least, Middle Turolian age for the origin of the Gargano faunas.

The different glirid species from Gargano clearly fit within the dental pattern of *Ramys* Garcia-Moreno. *Ramys multicrestatus* and its close relative *R. tenni* (not *Vasseuromys*) are

* tma : "tubercule medial antérieur" according to the nomenclature of the Murids by Michaux (1971).
** t_n : name of each cusp in the upper molars of the Murids, according to Michaux (1971).

Source : MNHN, Paris

common elements of the Vallesian and Early Turolian faunas (for the latter case, we have Dörn-Durkheim, Eichkogels, etc.). This datum also corroborates the Early Turolian origin of the Gargano faunas. In this case, the isolation process was probably linked to the tectonic evolution of the Adriatic Sea.

B. *Dental characteristics of the endemic glirids*

Size.

All the extant genera of glirids from the Western Mediterranean present endemic insular forms during the Late Neogene and Quaternary. The largest number of these correspond to the genus *Eliomys (Hipnomys, Eivissia, Maltamys, Tyrrhenoglis, Leithia)* but insular species have also been described for *Glis* (*G. major* from Oschiri, Sardinia) and *Muscardinus* (*M. cyclopaeus* from Cala Es Pou, Minorca). In addition, the endemic forms of *Pseudodryomys (Margaritamys, Carbomys)* and *Ramys* (*Stertomys* from Gargano), developed in the Miocene must also be mentioned. A tendency toward gigantism is the most generalized feature among these glirids. All the insular genera and species mentioned above are already much larger than their continental relatives. Sometimes, when there exists a long time-span record, a general increase in size can be observed in the successive species (*Hypnomys*, Gargano genus) although oscillations in size (*Hypnomys* in Majorca) or entry of small-sized continental immigrants (Sta. Margarida, Gargano) may also be possible. The degree of gigantism seems to be related to the surface of the island (Heaney, 1978). Thus, *Hypnomys* sp. from Ibiza is larger than any of the *Hypnomys* species. Moreover, *H. mahonensis* from Minorca is larger than *H. morpheus* from Majorca. It is also significant that the largest endemic dormouse is *Leithia* from Malta.

The cases of insular forms which display similar sizes to continental ones are very rare. The fauna from Ses Fontanelles (Ibiza) already seems to be of an insular kind: *Protatera* sp. is larger than the specimens of *Protatera algeriensis* which appear in the Spanish Late Miocene and aff. *Tyrrhenotragus* sp. is a small endemic antilopini. Nevertheless, *Eliomys* sp. fits well within the size of the Pliocene species *E. intermedius*. Another possibility is that the Ibiza *Eliomys* could be the descendant of the small species *E. truci*. In that case, an increase in size can also be postulated. The oldest known *Hypnomys* representatives (*H. waldreni* from Cap Farruxt and Cova de Canet) are already larger than the species from the continent. Even in cases of a lesser degree of morphological change (*Eivissia canarreiensis, Muscardinus cyclopaeus*) the size has considerably increased. The tendency to gigantism is not an exclusive characteristic of insular evolution in micromammals and it could also be linked to the development of dry conditions in continental environments (*Armantomys aragoniensis giganteus* from Las Planas IV, Spain, and *Muscardinus giganteus*, from Osztramos-3, Hungary).

Hypsodonty.

Whereas a general increment in hypsodonty is a generalized feature in the forms derived from *Eliomys (Hypnomys, Maltamys, Tyrrhenoglis, Leithia)* this is not the case for *Muscardinus cylopaeus* or *Glis major*. It is interesting to note that whereas *Eliomys* is an ubiquitous form, *Muscardinus* and *Glis* are usually associated with wooded environments. Hypsodonty is a character which appeared many times in continental glirids such as *Praearmantomys* and *Armantomys*. This character is thought to be associated with the adaptation to dry/open conditions.

Development of extra ridges outside the trigone.

This tendency appears in some *Eliomys* descendants like *Maltamys* and *Tyrrhenoglis* but is absent in the remainder (*Hypnomys, Eivissia* and *Leithia*, which maintain the basic *Eliomys* pattern). The presence of extra ridges outside the trigone in the Gargano lineage was certainly not the effect of insularity and they were probably already present in the continental ancestor (*Ramys multicrestatus*).

Isolation of the centrolophs.

This is a common characteristic in *Tyrrhenoglis* (*T. majori* Engesser), *Hypnomys* (*H. eliomyoides, H. morpheus*) and *Leithia* (*L. cartei*), being absent in *Maltamys* and *Eivissia*. This phenomenon is also observed in some Dryomyinae in the Lower Miocene (*Pseudodryomys* or closely related forms). The presence of this character in *Margaritamys* is not thought to be

Source : MNHN, Paris

caused by evolution in insularity conditions but to be the effect of a direct descent from these Lower Miocene Dryomyinae.

The labial isolation of the anterior centroloph (the posterior one tends to disappear) in the upper molars is usually complemented by the lingual fusion to the metaloph (*Hypnomys, Tyrrhenoglis* and *Maltamys*). This tendency is also observed in some Lower Miocene Dryomyinae related to *Pseudodryomys* (which would explain the presence of this character in *Carbomys* and *Margaritamys*). In *Leithia* there is a particular tendency of the protoloph to fuse with the metaloph anteriorly. In *Evissia*, none of these fusions are present.

Development of a continuous endolophid.

This kind of modification appears in some *Hypnomys morpheus* specimens and it seems to be a typical characteristic of *Tyrrhenoglis*. This is a surprising fact, since the development of a continuous endolophid in the lower molars is a rare case in the glirids, only present in some Lower Miocene species related to the genus *Glirudinus*.

Increasing width of lophs and lophids.

This is a common adaptation in *Hypnomys, Leithia, Maltamys* and *Tyrrhenoglis*, which display more robust lophs and lophids than their continental relatives. On the contrary, the relative width of the lophs is similar to the continental forms in *Evissia canarreiensis* and *Muscardinus cyclopaeus*. When *M. cyclopaeus* from Minorca is compared with *M. giganteus* from the Pliocene of Osztramos-3, it is surprising to discover that the continental species displays wider lophs than that from Minorca. An adaptation of *M. giganteus* to a more abrasive diet could explain this difference. Such a process also appears in some lineages in the Early Miocene (*Pseudodryomys, Praearmantomys, Armantomys*).

Variation in the shape of the molars.

The shape of the molars had clearly changed in *Hypnomys, Leithia* and *Maltamys*. In these cases, both upper and lower molars become longer than those of *Eliomys*. In *Maltamys* this tendency seems not to be so accentuated whereas *Evissia* maintains the similar *Eliomys* shape in the molars. Moreover, *M. cyclopaeus* is very close to *M. vireti* in this aspect.

Molarization of the premolars.

This process is evident in *Leithia, Maltamys, Glis major* and the Gargano specimens. On the contrary, no trace of molarization is apparent in *Evissia* or *M. cyclopaeus*, whereas there is scant development of the premolar in *Hypnomys* and *Tyrrhenoglis*.

Conclusion

The tendency to increase size is a common character in all the forms analyzed. Once a population becomes isolated, the evolution towards gigantism is very quickly developed. On the contrary, other characters seem to evolve gradually over large time periods (morphological characters). Finally, some other characters (continuous endolophids) are the result of a particular evolution in some forms. Thus, the resulting scheme of the whole process of dental evolution in insular conditions is the following:

— After isolation, the species undergoes a very rapid evolution, which only affects its size and it becomes much larger than the continental ancestor. This tendency to " gigantism " is thought to be a consequence of the absence of carnivores on the island (Thaler, 1973). The definitive dimensions are probably in inverse correlation with the surface area of the island (Heaney, 1978).

— In a second phase, there is a slow, gradual adaptation to the environmental conditions of the island. Most of the morphological characteristics in this phase (hypsodonty, extra ridges centrolophs, more robust lophs and lophids, more lengthened molars, molarized premolars) indicate an adaptation to very dry biotopes. This is also congruent with the dental evolution observed in *Myotragus* (a tendency to develop ever-growing incisors).

Source : MNHN, Paris

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Tooth Structure in *Stegolophodon, Eostegodon* and *Stegodon* (Proboscidea, Mammalia) : their Phylogenetic Relation

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ABSTRACT

The relationship between the genus *Stegolophodon* and the genus *Stegodon* is reexamined on the basis of fossil molars kept in the British Museum (Natural History) and of Japanese specimens. The Stegolophodont molars are characterized by the bunodont structure of the first and the second ridges which are similar to those of gomphotheres. On the other hand, lophodont structures are observed in all ridges of the stegodont molars. The molar of *Eostegodon* shows an intermediate stage between bunodonty and lophodonty and more resembles stegodont molars than stegolophodont molars. According to these results, it can be said that the genus *Eostegodon* Yabe is valid, and that it includes two species, *E. pseudolatidens* and *E. tsudai*. Stratigraphically, *Stegolophodon* is not much older than *Stegodon*, so it does not seem to be the ancestor of *Stegodon*. The occurrence of *Eostegodon* is confined to the lower or the middle Miocene in the Japanese Islands. These facts support the idea that the genus *Eostegodon* is the ancestor of the genus *Stegodon*. The family Stegodontidae includes two genera, *Stegodon* and *Eostegodon*.

RÉSUMÉ

Les relations entre le genre *Stegolophodon* et le genre *Stegodon* sont réexaminées à la lumière des molaires conservées au British Museum (Natural History) et des spécimens japonais. Les molaires stégolophodontes sont caractérisées par la structure bunodonte des première et seconde crêtes qui sont semblables à celles des gomphothères. Au contraire, on observe une structure lophodonte sur toutes les crêtes des molaires stégodontes. La molaire de *Eostegodon* présente un état intermédiaire entre les structures bunodonte et lophodonte tout en ressemblant davantage aux molaires stégodontes qu'aux molaires stégolophodontes. Selon ces résultats, on peut dire que le genre *Eostegodon* Yabe est valide, et qu'il comporte deux espèces, *E. pseudolatidens* et *E. tsudai*. Stratigraphiquement *Stegolophodon* n'est pas plus ancien que *Stegodon*, de sorte qu'il ne paraît pas en être l'ancêtre. La présence de *Eostegodon* est limitée au Miocène inférieur et moyen des îles japonaises. Ces faits renforcent l'hypothèse selon laquelle le genre *Eostegodon* serait l'ancêtre du genre *Stegodon*. La famille des Stegodontidae inclut donc deux genres, *Stegodon* et *Eostegodon*.

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Introduction

The Stegodontidae is one of the families of the Proboscidea and includes two genera, *Stegolophodon* and *Stegodon*. These fossil elephants have been principally discovered in east and south Asia, and they are very important members of the Neogene and the Quaternary faunas in these areas. Fossils of *Stegolophodon* and *Stegodon* have been studied by many palaeontologists interested in the problems of the origin of Elephantidae (Falconer & Cautley, 1846; Schlesinger, 1917; Matsumoto, 1926; Osborn, 1936 and 1942; Maglio, 1973; Tobien, 1975; Taruno, 1985). Their molars have an intermediate form between those of the primitive proboscideans and the advanced ones. In the Japanese Islands we can find many kinds of fossil elephants from the various stratigraphic horizons ranging from the lower Miocene to the uppermost Pleistocene.

Stegolophodon pseudolatidens and *Stegolophodon tsudai* are known from the lower and the middle Miocene (mainly N8 after Blow's zoning). They were treated as the oldest members of *Stegolophodon* (Shikama & Kirii, 1956; Shikama & Yanagisawa, 1971; Takai & Fujii, 1961; Kamei & Kamiya, 1981). Yabe (1950) considered that *S. pseudolatidens* represents a different group from *Stegolophodon* of India and Burma, and proposed the new genus *Eostegodon*, which would be the ancestor of *Stegodon*. But many workers do not use this name. We reexamined the molars of the Japanese *Stegolophodon* (or *Eostegodon*; we use this name in the following) in comparison with the molars of *Stegolophodon* from southeast Asia. We also studied the *Stegodon* molars in relation to *Stegolophodon*. All the specimens examined are the type specimens or the referred ones.

Observations

A. *Morphological Study*

Seven specimens kept in the British Museum (Natural History) were reexamined and compared with Japanese specimens. In this work, the morphology of the mesial part of the third molar, especially the first and the second ridges were examined in detail because it may be said that these two ridges are homologous to the main four cusps in the usual mammalian molars (Tobien, 1975).

The results of the examination are shown in Figs. 1, 2 and 3, and Table 1. According to these results, it is obvious that the molars of *Stegolophodon* (from India and Burma) are characterized by the bunodont stucture of the first and the second ridges which are similar to those of gomphotheres. In the stegodont molars, all ridges have lophodont structures. The molars of *Eostegodon* have an intermediate structure between bunodonty and lophodonty, and have more similarity to stegodont molars than to those of stegolophodonts.

B. *Histological Study*

Histological studies were made by means of light and scanning electron microscopy, and the enamel structure of some specimens was mainly observed. In the first molar of *Eostegodon pseudolatidens*, the enamel is about 2 or 3 millimeters in thickness and divided into two parts, inner and outer. The growth lines are visible in the outer part but are not clear in the inner part (Pl. 1, 1 and 2). Such " bilayering " in the enamel is often observed in the case of advanced proboscideans, for instance *Stegodon (Parastegodon) akashiensis, Palaeoloxodon naumanni* and so on (Pl. 1, 3 and 4). It is regarded as a factor characterizing the molars in advanced proboscideans.

In the molar of *Stegodon akashiensis*, the enamel is composed of two layers. In this material the outer layer does not have distinct growth lines, but in the inner one they are well visible. In the molar of *Stegolophodon latidens* from Burma the enamel has a large thickness, of about five or six millimeters. Two layers in the enamel can be observed, but it is not so obvious. Bilayering of the enamel is formed by different orientation of the Hunter-Schreger's bands. In the longitudinal section of the molar of *Eostegodon pseudolatidens*, arrangement of the Hunter-Schreger bands is oblique to the dentino-enamel junction by about sixty degrees in the inner layer, but in the outer layer it suddenly becomes approximately perpendicular to the dentino-enamel junction or the surface of the enamel. This is also recognized in the case of *E. tsudai*. Such a

Source : MNHN, Paris

TABLE 1. Criteria of *Stegolophodon*, *Eostegodon* and *Stegodon* (Taruno, 1985).

Characters	*Stegolophodon*	*Eostegodon*	*Stegodon*
Structure of the 1st & 2nd ridges of M3	bunodont pattern	intermediate between bunodont & lophodont	lophodont pattern
Median sulcus of M3	distinct in mesial part	distinct in mesial part	indistinct in advanced species
Distobuccal crest of protocone of $^2M^3$	exists	weak	absent
Conule of the 2nd ridge of M3	exists	absent	absent
Number of cones and conules	3	4	6 or more
Id. ($^2M^2$, 2nd ridge)	4	7	6 or more, in many cases 8 or more
Number of ridges ($^2M^1$)	5-6	4-5	6-15
Id. ($^2M^2$)	4	4	5-9
Projection of the inner layer of enamel at the abrasion surface	not observed		observed
Cementum	slightly developed	slightly developed [1]	well developed
Angulus mandibulae	flat linguobuccally, expanded infracaudally	?	round

1 modified in this study

pattern is well developed in the enamel of *Stegodon*.

On the other hand, it is known that the shape of the enamel prisms is closely related to the evolutionary stage in Proboscidea (Kozawa, 1978). In tranverse sections, the enamel prisms have a key-hole shape in the primitive probosciceans while in the advanced ones, the enamel prisms have a ginkgo-leaf pattern (Pl. 1, 5 and 6). The enamel prisms of *Eostegodon pseudolatidens* have mainly the key-hole shape in the transverse section. Width of each prism is five or six microns, and shows the pattern 3 after Boyde (1969). In some cases, enamel prisms having laterally elongated or ginkgo-leaf shapes are found (Pl. II, 1, 2 and 3). Width of the prism is six or seven microns, which is slightly larger than that of the key-hole shaped prisms. In the other species of *Eostegodon*, *E. tsudai*, a similar pattern can be recognized. The enamel is mainly composed of key-hole shaped prisms whose width is six or eight microns, but often includes laterally elongated or ginkgo-leaf prisms with a width of seven or eight microns. In the specimen of *S. latidens*,

Source : MNHN, Paris

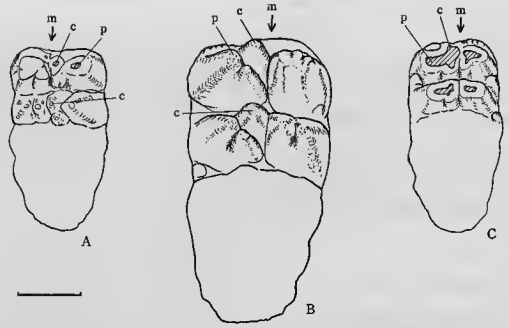

FIG. 1. — *Stegolophodon* spp. Occlusal views of the first and second ridges of the third upper molar; c = conule; m = median sulcus or conulid; p = protocone.
A, *S. latidens* (Clift), M^3, M29713, lectotype by Osborn (1942); B, *S. cauleyi* (Lydekker), ^3M, M2705, lectotype by Osborn (1942); C, *S. lydekkeri* Osborn, ^3M, M7225, holotype. Scale shows 5 cm.

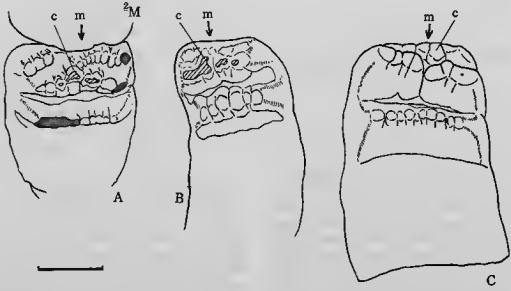

FIG. 2. — *Stegodon* spp. Occlusal views of the first and second ridges of the third molar; c = conule or conulid; m = median sulcus.
A, *S. insignis* (Falconer & Cautley), M^3, 36735, referred specimen; B: *S. elephantoides* (Clift), $_3M$, M10516, lectotype by Osborn (1942); C, *S. zdansky* Hopwood, M_3, M14816, cast of holotype. Scale shows 5 mm.

Source : MNHN, Paris

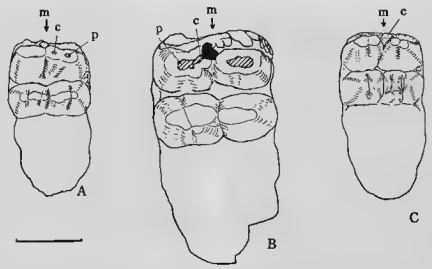

FIG. 3. — *Eostegodon* spp. Occlusal views of the first and second ridges of the third molar; c = conule or conulid; m = median sulcus; p = protocone.
A, *E. pseudolatidens* Yabe, ^{3}M, holotype; B, *E.* cf. *tsudai* Shikama & Kirii, ^{3}M, Iwaki specimen; C, *E. pseudolatidens* Yabe, M_3, Tochizu specimen. Scale shows 5 mm.

the enamel is composed of key-hole shaped prisms. Their width is six or seven microns, and sometimes a laterally elongated shape can be observed (Pl. II, 4, 5 and 6).

CONCLUSION

The molar teeth of the Japanese *Stegolophodon (Eostegodon)*, *Stegolophodon* and *Stegodon* were examined in order to clarify their phylogenetic relationship.

Eostegodon has molar teeth which show an early stage of lophodonty, although its occurrence is confined to the lower and middle Miocene. Molars of *Stegolophodon* from the young deposits in India and Burma show a bunodont-like pattern.

These results support the proposal by Yabe (1950) that the genus *Eostegodon* represents a different group from the genus *Stegolophodon*, and is the ancestor of the genus *Stegodon*.

The results obtained by the histological study are consistent with those resulting from morphological ohservations.

ACKNOWLEDGMENTS

We express gratitude to Drs. A. W. Gentry, J. J. Hooker and A. P. Currant of the British Museum (Natural History) for giving us the chance to examine the important specimens of the museum. We are also thankful to Prof. T. Kamei, Dr. Y. Kozawa and Mr. H. Saegusa for their kind support in our work.

Source : MNHN, Paris

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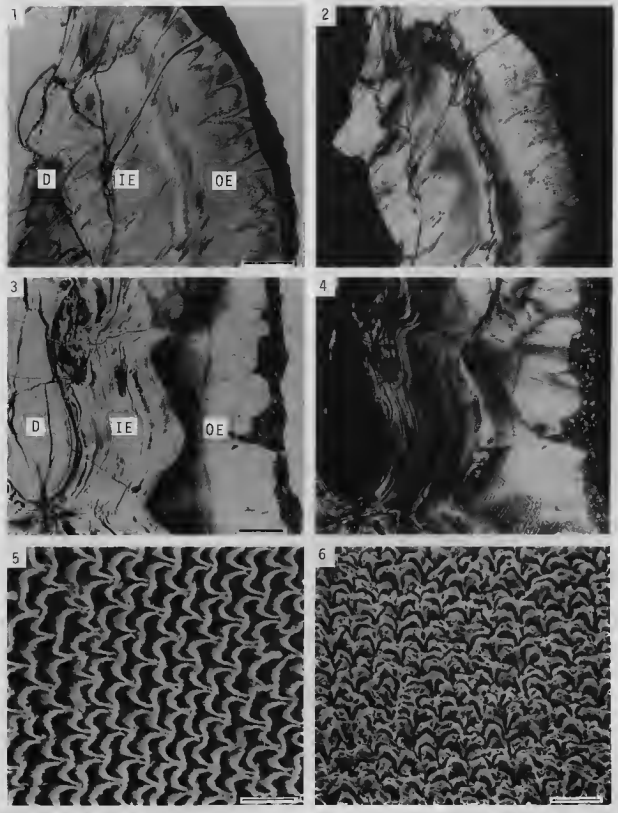
Pl. 1. — 1. Longitudinal section of enamel of *Eostegodon pseudolatidens*. D = dentine; IE and OE = enamel; parallel nicols, scale shows 1 mm.
2. Same section (crossed nicols).
3. Horizontal section of enamel of *Stegodon akashiensis, (Parastegodon)*. D = dentine; IE and OE = enamel; parallel nicols; scale shows 1 mm.
4. Same section (crossed nicols).
5. Scanning electron microscopic image of the enamel of *Palaeoloxodon naumanni* (from the upper Pleistocene in Japan). Scale shows 10 μm.
6. Scanning electron microscopic image of the enamel of *Stegodon (Parastegodon) sugiyamai*. Scale shows 10 μm.

Source : MNHN, Paris



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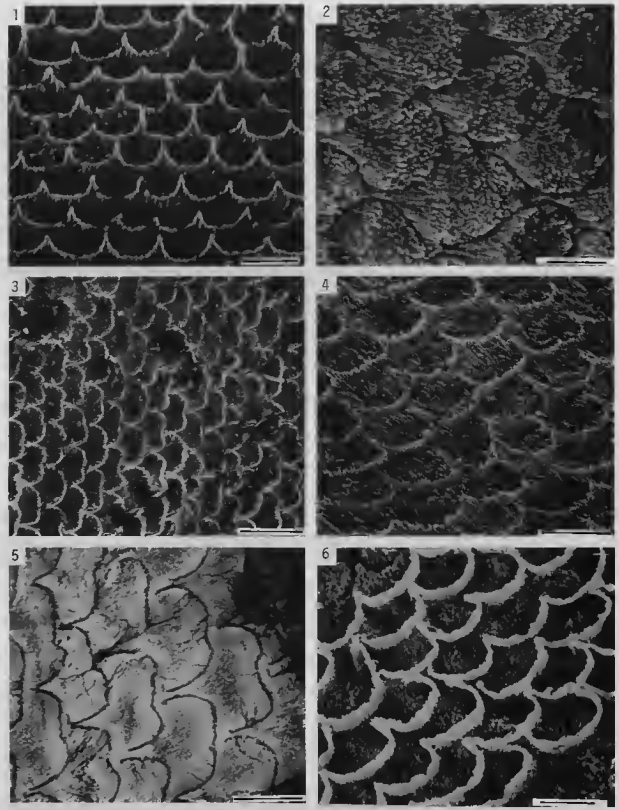


PL. II. — Scanning electron microscopic images of enamel of *Eostegodon* and *Stegolophodon*.
1-3. *Eostegodon pseudolatidens*.
4-5. *Eostegodon tsudai*.
6. *Stegolophodon latidens*.
Scale shows 10 μm (1, 3, 4, 6) and 5 μm (2,5).

Source : MNHN, Paris

Morphological Variations of the First Upper Molar in the Genus *Martes* (Carnivora, Mustelidae)

M. WOLSAN

ABSTRACT

Polymorphism in the occlusal surface of the lingual lobe of the first upper molar is described by means of morphotypes in some populations of *Martes zibellina* (n = 725), *M. martes* (n = 511), *M. zibellina* × *M. martes* (n = 37), *M. americana* (n = 27), *M. foina* (n = 206), and *M. flavigula* (n = 48). The polymorphism consists first in the occurrence of an occluso-basal depression of variable depth in about half of the length of the ridge running postero-lingually from the medial portion of the anterior cingulum; second in the presence of some accessory enamel elevations, forming minor ridges and cuspules variable in size and shape, developed along two curves branching from the posterior portion of the foregoing ridge and crossing the postero-lingual part of the occlusal surface to reach the posterior cingulum. The same morphological pattern affects either both sides or one side only, usually complying with a general rule: the less frequent a morphotype the more likely it is for it to occur unilaterally. Frequency distributions for the morphotypes differ qualitatively and quantitatively, mostly with a statistical significance, both between the species and at a population level. It is suggested that the characters involved in the polymorphism are homologous, respectively, with a depression separating the paraconule and the protocone, and with the protocone-metaconule-posterior cingulum and protocone-hypocone-posterior cingulum crests in a primitive eutherian tribosphenic upper molar. Supporting evidence for this hypothesis is presented.

RÉSUMÉ

Le polymorphisme de la surface occlusale du lobe lingual de la première molaire supérieure est décrit d'après des morphotypes pris dans des populations de *Martes zibellina* (n = 725), *M. martes* (n = 511), *M. zibellina* × *M. martes* (n = 37), *M. americana* (n = 27), *M. foina* (n = 206) et *M. flavigula* (n = 48). Ce polymorphisme consiste d'une part en la présence d'une dépression occluso-basale, de profondeur variable, développée sur environ la moitié de la crête qui court postéro-lingualement à partir de la portion médiale du cingulum antérieur; d'autre part, en la présence de quelques éminences accessoires d'émail qui forment des crêtes mineures et des cuspules de taille et de forme variables, disposées le long des deux courbes partant de la portion postérieure de la crête précédente et traversant la partie postéro-linguale de la surface occlusale pour atteindre le cingulum postérieur. La même morphologie peut s'observer sur un ou deux côtés de la mâchoire ; en règle générale, il est d'autant plus probable qu'un morphotype se trouve d'un seul côté qu'il est plus rare. Les distributions de fréquence des morphotypes diffèrent qualitativement et quantitativement ; elles sont le plus souvent statistiquement significatives, que ce soit entre les espèces ou entre les populations d'une même espèce. Les caractères impliqués dans le polymorphisme peuvent être homologués, respectivement, à une dépression séparant le paraconule et le protocone, et aux crêtes reliant protocone-métaconule-cingulum postérieur et protocone-hypocone-cingulum postérieur sur une molaire supérieure tribosphénique de Mammifère euthérien primitif. Les faits soutenant cette hypothèse sont présentés.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris*, (série C) **53** : 241-254.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

As far back as 1912, Miller paid attention to morphological variability in the occlusal surface of the first upper molar lingual lobe in the European pine marten. He noted: " inner portion of crown with a slightly curved, ridge-like antero-external cusp (usually notched or partly divided into two), the surface elsewhere finely wrinkled; in some specimens a minute tubercle, perhaps representing the hypocone, occurs near posterior border of crown in region of constriction between outer and inner portions ". Pavlinov (1974) found a well developed crescent-shaped ridge running across the waist of M^1 from the anterior to posterior cingula in two European pine martens of the Soviet Union. And lastly Wolsan *et al.* (1985) characterized both variation and asymmetry patterns in the cheek dentition of the European pine and stone martens from Poland, introducing twelve morphotypes of two different groups for description of morphological variations in the lingual portion of M^1. Since then the senior author has raised the total sample size for the Polish populations, and undertaken a survey of permanent dentitions in some other populations of *Martes martes* and *M. foina* as well as in those of *M. zibellina*, *M. zibellina* × *M. martes*, *M. americana*, and *M. flavigula*. This paper presents the results of the author's investigations with respect to polymorphism of the M^1 lingual lobe.

Material and Method

The study is based on a survey of the first upper permanent molars (M^1) in a total of 1554 recent specimens of both sexes of the genus *Martes* Pinel, 1792. The five species studied include: the sable, *M. zibellina* (Linnaeus, 1758), the European pine marten, *M. martes* (Linnaeus, 1758), the American pine marten, *M. americana* (Turton, 1806), the stone marten, *M. foina* (Erxleben, 1777), and the yellow-throated marten, *M. flavigula* (Boddaert, 1785). The sable specimens come from the Ural Mts. region (n = 147; Ural'skaya Oblast', Permskaya Oblast', Pechoro-Ilychskiy Nature Reserve, and Kondo-Sos'vinskiy Nature Reserve), central Asia (n = 224; U.S.S.R.: Irtysh region, Altai, Sayan, Krasnoyarskiy Kray, Irkutskaya Oblast', and Buryat-Mongol A.S.S.R.), Far East (n = 48; U.S.S.R.: Amurskaya Oblast', Khabarovskiy Kray, Primorskiy Kray, and Sakhalin), and Kamchatka (n = 306). The European pine martens were caught in Poland (n = 230), Ukraine (n = 25), the central part of the European U.S.S.R. (n = 47; Moskovskaya Oblast'), the northern part of the European U.S.S.R. (n = 117; Novgorodskaya Oblast', Leningradskaya Oblast', Finno-Karelian A.S.S.R., and Arkhangel'skaya Oblast'), Caucasus Mts. region (n = 84; Kuban' region, Caucasus Mts., and Georgian S.S.R.), and Ural Mts. region (n = 8; Bashkir A.S.S.R.). The American pine martens involve the Alaska and Montana populations (n = 27) and the stone martens examined refer to those of Poland (n = 54), Ukraine (n = 55), Caucasus Mts. region (n = 84; Caucasus Mts., Georgian S.S.R., Azerbaidzhan S.S.R., and Armenian S.S.R.), and central Asia (n = 13; Kopet Dagh, Pamirs, Tien Shan, Altai, and Mongolia). The yellow-throated martens were hunted in the Far East of the U.S.S.R. (n = 48; Primorskiy Kray). In addition, 37 specimens of the hybrid *M. zibellina* × *M. martes* from the Ural Mts. region (Pechoro-Ilychskiy Nature Reserve) were available.

The skulls examined belong to the collections of the Zoological Museum, Moscow State University, Moscow, the Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad, the Institute of Zoology, Academy of Sciences of the Ukrainian S.S.R., Kiev, the Mammals Research Institute, Polish Academy of Sciences, Bialowieża, the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Cracow, the Department of Systematic Zoology, A. Mickiewicz University, Poznań, and to the private collection of A. L. Ruprecht.

Two groups of morphotypes involving the occlusal surface of the first upper molar lingual lobe have been studied. The group D (Wolsan *et al.*, 1985) deals with the postero-lingual region of M^1 (Fig. 1, I). The variation in this crown region consists in the occurrence of some accessory elevations of the enamel surface. These elevations form minor ridges and cuspules variable in size and shape, developed along two curves branching from the posterior part of the ridge which runs postero-lingually from the medial

Source : MNHN, Paris

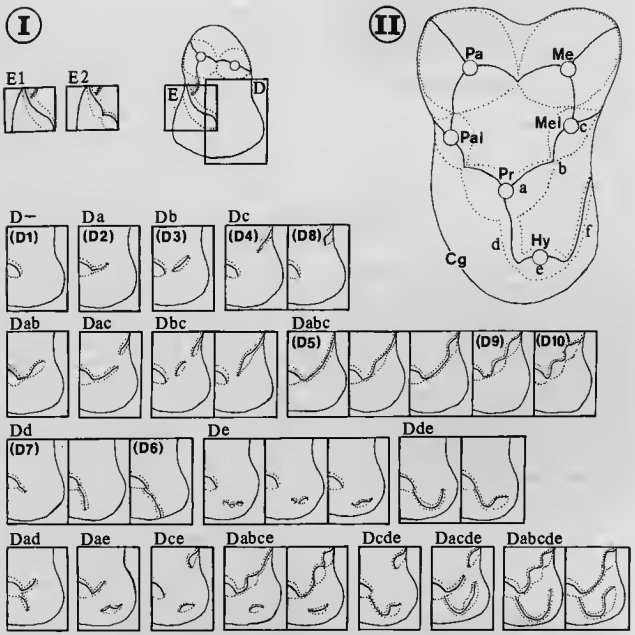


FIG. 1. — I. Diagrams of a typical first upper molar in *Martes* and of morphotypes of groups D and E. The terms of D morphotypes used by Wolsan *et al.* (1985) are given in parentheses.
II. A hypothetical pattern of the upper molar occlusal surface in a primitive eutherian ancestor of the lineage of *Martes*. Cg = cingulum; Hy = hypocone; Me = metacone; Mel = metaconule; Pa = paracone; Pal = paraconule; Pr = protocone; a, b, and c indicate, respectively, anterior, medial, and posterior regions of the protocone-metaconule-posterior cingulum crest and d, e, and f are, respectively, those of the protocone-hypocone-posterior cingulum crest.

Source : MNHN, Paris

portion of the anterior cingulum and crosses the postero-lingual part of the occlusal surface to reach the posterior cingulum. Three regions have been distinguished both in the buccal and lingual curves: the anterior (designated a and d), medial (b and e), and posterior (c and f) ones (Fig. 1, II). The morphotypes are named according to the designation of the curve regions in which the elevations occurred. The absence of any elevation is termed D-.

The group E (Wolsan *et al.*, 1985) deals with a distinct ridge running postero-lingually from the medial portion of the anterior cingulum (Fig. 1, I). The variation in this ridge is manifested by the occurrence of a V- or U-shaped occluso-basal depression of variable depth in about half of the length of the ridge (E2). The absence of the depression is indicated by the morphotype E1.

Both the left and right teeth of each specimen have been included in morphotype counting because the morphotypes are frequently asymmetric, particularly those that are rare. The differences between the total number of skulls under study and the expected number of M^1s (twice as many) and those given in figures and tables are due to the absence of some teeth or the heavy wear which prevents the definite determination of a morphotype.

The part of the data concerning the Polish populations of *M. martes* and *M. foina* was published by Wolsan *et al.* (1985). But since then total sample sizes for these populations have been increased and the pooled data are shown in the present paper.

Results

For the morphotypes of groups D and E, no statistically significant differences ($P > 0.05$) between male and female frequency distributions have been discovered. Hence, the data for both the sexes are pooled in figures and tables.

A. *Morphotypes of Group D*

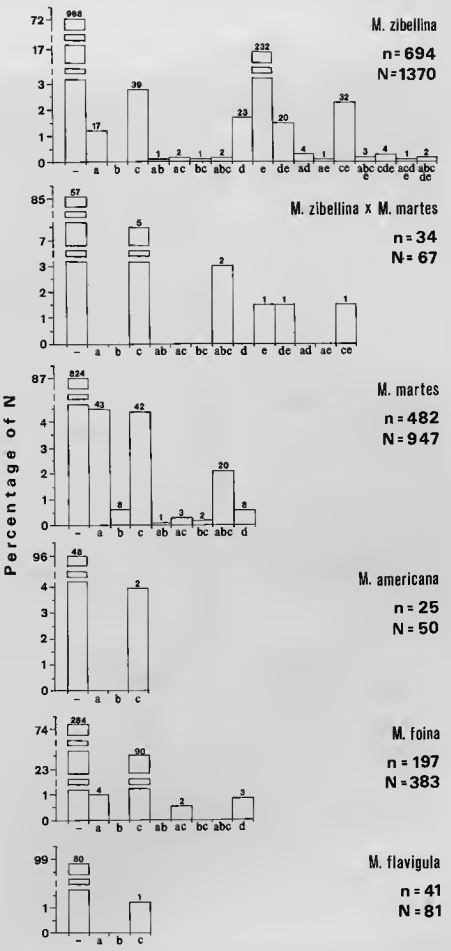
The members of the genus *Martes* examined show 18 of the 64 theoretically possible morphotypes of group D (Fig. 1). Most common of the morphotypes are D- and Dc, which are present in all of the studied species (Fig. 2). The morphotypes Da, Dac, and Dd occur in three of the species, namely in *M. zibellina*, *M. martes*, and *M. foina*; Dab, Dac, Dbc, and Dabc are present only in the two former species. The one and only species involved in the occurrence of the morphotype Db is *M. martes*, and that concerned by the remaining D morphotypes here distinguished is *M. zibellina*. The hybrid *M. zibellina* × *M. martes* shows three morphotypes common in the native species, to wit, D-, Dc, and Dabc, while the others (De, Dde, and Dce) are to be found also only in *M. zibellina*.

In all the species under study the morphotype D- is clearly dominant, ranging from 72.0 % in *M. zibellina* to 99.0 % in *M. flavigula* (Fig. 2). Of the non-D- morphotypes, only Dc in *M. foina* and De in *M. zibellina* are relatively frequent (23.5 % and 17.0 %, respectively). The frequencies of the remaining morphotypes range from 0 to 7.5 %, not exceeding 1 % for the most part.

The greatest diversity in the D morphotypes has been found in *M. zibellina* (Fig. 2). This species shows sixteen various non-D- morphotypes, occurring with a total frequency of 28.0 % (central Asia — 37.5 %, Kamchatka — 33.8 %, Far East — 27.0 %, and Ural Mts. region — 4.5 %). The most frequent of these morphotypes is De (17.0 %), followed by Dc (2.8 %), Dce (2.3 %), Dd (1.7 %), Dde (1.5 %), Da (1.2 %), and ten other morphotypes (under 0.3 % each). *M. martes* shows eight various non-D- morphotypes, occurring with a total frequency of 13.0 % (Caucasus Mts. region — 28.4 %, Ural Mts. region — 26.7 %, Poland — 10.7 %, northern part of the European U.S.S.R. — 10.4 %, central part of the European U.S.S.R. — 6.0 %, and Ukraine — 0 %). The most frequent are the Da (4.5 %) and Dc (4.4 %) morphotypes, followed by Dabc (2.1 %) and five others (under 0.7 %

FIG. 2. — Percentage frequency distributions of the morphotypes of group D. Numbers given above the rectangles of the histograms show absolute frequencies of the morphotypes for the given rectangles. N and n are the numbers of scored teeth and skulls, respectively.

Source : MNHN, Paris


M. zibellina
n = 694
N = 1370
M. zibellina x M. martes
n = 34
N = 67
M. martes
n = 482
N = 947
M. americana
n = 25
N = 50
M. foina
n = 197
N = 383
M. flavigula
n = 41
N = 81
Percentage of N
Morphotypes of group D
Source : MNHN, Paris

each). The hybrid *M. zibellina* × *M. martes* shows five various non-D- morphotypes, occurring with a total frequency of 14.9 %. The most frequent of these morphotypes is Dc (7.5 %), followed by Dabc (3.0 %) and De, Dde, and Dce (1.5 % each). *M. foina* shows four various non-D- morphotypes, occurring with a total frequency of 25.8 % (central Asia — 50.0 %, Caucasus Mts. region — 30.6 %, Poland 19.2 %, and Ukraine — 18.4 %). The most frequent is the morphotype Dc (23.5 %), followed by Da (1.0 %), Dd (0.8 %), and Dac (0.5 %). Both *M. americana* and *M. flavigula* show only one of the non-D- morphotypes, that is Dc, occurring with frequencies of 4.0 % and 1.0 %, respectively.

With the exception of some very rare morphotypes, for all the species studied the morphotype D- is apparently the most symmetrical in occurrence, with frequencies of unilateral occurrences ranging from 2.5 % in *M. flavigula* to 13.9 % in *M. zibellina* (Table 1). The bilateral occurrences outnumber the unilateral ones exclusively for Dc in *M. foina* and *M. zibellina*, De in the latter species, and some very rare morphotypes (Dac in *M. zibellina*, Dabc in *M. zibellina* × *M. martes*, and Da and Dac in *M. foina*). Most of the remaining morphotypes show a great amount of left-right asymmetry in occurrence.

Of the six curve regions distinguished, namely a, b, and c for the buccal curve and d, e, and f for the lingual one (Fig. 1, II), solely the latter in all the species under study has appeared not to be occupied by the accessory enamel elevations (Fig. 3). From the remaining regions, only c is

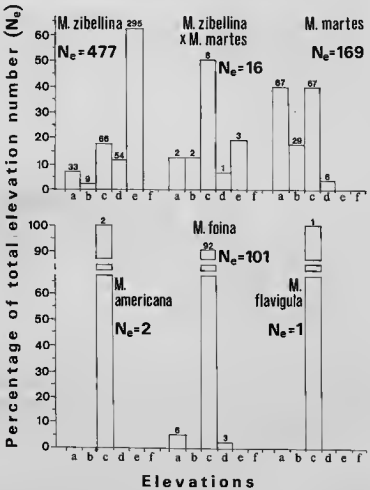


FIG. 3. — Percentage frequency distributions of the enamel elevations a, b, c, d, e, and f. Numbers given above the rectangles of the histograms show the absolute frequencies of the elevations for the given rectangles.

Source : MNHN, Paris

involved in the occurrence of the elevations in all of the species. The enamel elevations developed in the a and d regions, namely the a and d elevations, are to be found in three of the species, that is, in *M. zibellina*, *M. martes*, and *M. foina*. The only species showing the b elevations are *M. zibellina* and *M. martes*, the former being the only one with the elevation e. The hybrid *M. zibellina* × *M. martes* is affected by the four various kinds of enamel elevations common to the native species (a, b, c, and d) and by e, exclusive to *M. zibellina*.

In other words, five of the six curve regions distinguished are occupied by the enamel elevations in *M. zibellina* (Fig. 3). The most frequently affected is the region e (61.8 %), followed by c (18.0 %), d (11.3 %), a (6.9 %), and b (1.9 %). Four of the regions exhibit the elevations in *M. martes*, with the regions a and c the most frequently affected (both 39.6 %), followed by b (17.2 %) and d (3.6 %). Five various kinds of elevations have been recorded in the hybrid *M. zibellina* × *M. martes*, with c as a most frequent one (50.0 %) and the others occurring at frequencies 18.8 % (e), 12.5 % (both a and b), and 6.3 % (d). Three kinds of the elevations have been discovered in *M. foina*, with the elevation c being a dominant one (91.1 %) and the remaining two as much more scarce (a — 5.9 % and d — 3.0 %). *M. americana* and *M. flavigula* show exclusively the c elevation.

Most of the enamel elevations distinguished usually occur on one side only (Table 2). Those for which the bilateral occurrences outnumber the unilateral ones are the elevations c in *M. foina*, e in *M. zibellina*, and some very scarce ones, namely a in *M. foina* and *M. zibellina* × *M. martes* and b in the latter.

B. *Morphotypes of Group E*

All of the species under study show the two E morphotypes distinguished (Fig. 4). The morphotype E2 is more frequent in *M. zibellina*, *M. zibellina* × *M. martes*, *M. martes* (exclusive of the Ural Mts. region population), and in the Caucasus Mts. region population of *M. foina*. For the remaining species and populations under study, the morphotype E1 prevails. Among fifteen paired combinations, which may be arranged from the total frequency distributions of the E morphotypes for the five species examined, and for the hybrid *M. zibellina* × *M. martes*, only two, namely *M. zibellina* — *M. zibellina* × *M. martes* and *M. americana* — *M. flavigula*, show no statistically significant differences ($P > 0.05$). Significant differences have been discovered for all the sympatric populations, except those of the Caucasus Mts. region (*M. martes* and *M. foina*).

All four populations of *M. zibellina* are roughly similar with respect to the frequency distributions of the morphotypes of group E (Fig. 4). However, when the frequency distributions were compared by 2 × 2 chi-square contingency tests, the insignificant differences ($P > 0.05$) appeared only between the Far East and Kamchatka populations. The E frequency distributions are similar in general outline for *M. martes* as well, apart from that of the Ural Mts. region population, which distinctly differs from the others. The differences of statistical significance ($P < 0.05$) occur both between the northern part of the European U.S.S.R. and Caucasus Mts. region populations and for all of the paired combinations involving the Ural Mts. region and Polish populations. Analogically, one of the populations, namely that of the Caucasus Mts. region, markedly differs as regards the E frequency distribution from the remaining ones in *M. foina*. In this species, however, the chi-square test shows no significant differences at a 0.05 level only between the Polish and Ukrainian populations.

Both the morphotype E1 and E2 usually occur on the left and right sides simultaneously (Table 3). The unilateral occurrences exceed in number the bilateral ones merely in some populations of *M. zibellina* (Far East, E1), *M. martes* (northern part of the European U.S.S.R. and Poland, E1), and *M. foina* (Poland, E2).

Discussion

The morphological variations in the occlusal surface pattern of the first upper molar lingual lobe, described by the morphotypes of groups D and E, show an evident regularity with respect to the site of appearance and the form. The occlusobasal depression, essential for the morphotype E2, has always occurred in some half of the

Source : MNHN, Paris

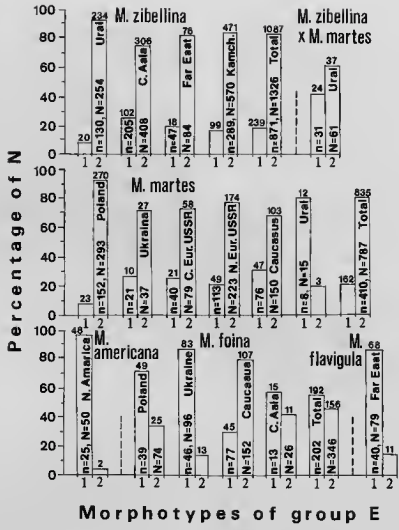


FIG. 4. — Percentage frequency distributions of the morphotypes of group E. Numbers given above the rectangles of the histograms show absolute frequencies of the morphotypes for the given rectangles. N and n are the numbers of scored teeth and skulls, respectively.

length of the ridge running postero-lingually from the medial portion of the anterior cingulum. The enamel elevations involved in the non-D-morphotypes have been developed exactly along two curves running from the posterior portion of the foregoing ridge towards the posterior cingulum (Fig. 1). No other accessory structures have been revealed on the occlusal surface of the M^1 lingual lobe, except some fine enamel wrinkles occasionally present on the cingulum only, or running concentrically from it towards the posterior portion of the ridge.

The morphotypes are common to the members studied of the genus *Martes*. Both E1 and E2, and from among the D morphotypes, D- and Dc, have been observed in all the species under study (Figs. 2 and 4). The frequencies of their occurrences, however, have been different. The species differ from each other both qualitatively and quantitatively as regards the remaining morphotypes. Those differences, though expressed to a lesser degree, are to be found at a population level as well. In addition, the frequencies of the morphotypes seem to show a clinal pattern in distribution. For instance, for *M. foina* the D-frequency generally increases westwards of cen-

Source : MNHN, Paris

tral Asia (central Asia — 50.0 %, Caucasus Mts. region — 69.4 %, Ukraine — 81.6 %, and Poland — 80.8 %) and for *M. martes* that of E2 is subject to gradual reduction with the distance from Poland (Poland — 92.2 %, northern part of the European U.S.S.R. — 78.0 %, central part of the European U.S.S.R. — 73.4 %, Ukraine — 73.0 %, Caucasus Mts. region — 68.7 %, and Ural Mts. region — 20.0 %) (Fig. 4).

Finally, the frequency distribution for the two groups of morphotypes in the Ural Mts. region population of the hybrid *M. zibellina* × *M. martes* are clearly of a transitional pattern as compared with those of the sympatric populations of *M. zibellina* and *M. martes*. For example, the D- frequencies amount to 85.1 %, 95.5 %, and 73.3 %, respectively, and those of E2 are, correspondingly, 60.7 %, 92.1 %, and 20.0 % (Fig. 4).

All the facts mentioned above support the idea that the characters involved in the D and E morphotypes are hereditary. The same morphological pattern affects either both sides or one side only, usually complying with a general regularity: the more frequent a morphotype, the lesser asymmetry there is in its occurrence (Tables 1 and 3) (cf. Wolsan *et al.*, 1985). The above is also true for the curve regions: the less frequently a region is occupied by enamel elevations, the more likely it is for these elevations to occur unilaterally (Table 2). Consequently, apart from the genetic factors, also some environmental ones acting on one side of an individual, are important in determining the morphotype.

Both the foregoing findings and polymorphism in size, shape, and occurrence of the enamel elevations studied, with some preferential curve regions (Figs. 1 and 3), suggest that a threshold mechanism, most probably connected with size, is involved in development of these elevations. The effect of such threshold mechanisms on tooth development seems to be a common phenomenon in mammals. The third upper and lower molars in some strains of inbred mice (Grüneberg, 1951, 1965, 1976; Searle, 1954a, 1954b, 1957; Grewal, 1962; Grüneberg *et al.*, 1972), the third lower premolar in *Ursus arctos* Linnaeus, 1758 (Kurtén, 1953), and the second upper one in *Felis bengalensis* Kerr, 1792 (Glass & Todd, 1977) may serve as examples. The threshold mechanisms operate exclusively at a certain stage in development. Those tooth structures which have reached the threshold continue to develop, while the others fail to develop further (e.g. Searle, 1960). Therefore, for thresholds connected with size, the smaller the size of a developing structure the more likely it is to atrophy. Consequently, the more frequent a structure in a population the more probable it was for it to be well developed at the critical threshold stage. Thus it seems possible to reconstruct with a high probability the morphology of the occlusal surface in the *Martes* first upper molar before and at the critical threshold stage, on the base of the knowledge of morphological patterns of this surface in the completely developed teeth and of their frequency distributions.

The enamel elevations appearing in the c region in the examined members of *Martes* usually resemble a small cusp in form. Similar minute cusps have sometimes occurred in the e region as well. In the other cases and also always for the a, b, and d regions, some enamel banks or ridges have been developed, varying in shape and length for the two former regions and for the latter being always narrow and low (Fig. 1, 1). The region the most frequently occupied by the elevations is c in all the species but one, namely *M. zibellina*, in which it is outnumbered by e. The next most frequent is the a region in most cases, generally followed by d. The b elevation is relatively scarce and no elevations have occurred in the f region (Fig. 3). It seems therefore very probable that the complete abc and def elevations are present in the *Martes* first upper molars at an early stage of their development, before the operating of a threshold mechanism. Some portions of the two elevations would be strongly developed, some others, poorly, resulting in the presence of swellings and depressions, respectively. The swellings, usually cusp-like, would occupy the c and e regions and the depressions would occur in the b and d (valleys) and a and f (slopes) ones. The buccal elevation would be generally stronger than the lingual one (Fig. 1, 1). The qualitative and quantitative differences in frequency distributions between individuals, populations, and finally between the species of *Martes*, would be due to both differences in morphological patterns at the critical threshold stage, and modifications of the threshold, which remains under a strong genetic control.

There are two possible explanations for the morphological variation of the M^1 lingual lobe in the genus *Martes*: the first would be that the

Source : MNHN, Paris

characters involved in this variation are caused by the influence of genes originated as a result of some relatively recent mutation or mutations; then they would be analogous to or apomorphous with respect to those of a primitive eutherian tribosphenic upper molar; the second explanation would be that these characters are inherited from some eutherian mammals of the late Cretaceous and early Cenozoic, and so they would be homologous with or plesiomorphous relative to those of their upper molars (Fig. 1, II).

The characters essential for the morphological variations under study occur in all of the examined species, which suggests that they are inherited from their common ancestor. It seems to be unlikely that we are dealing with a homoplastic similarity. That patristic characters are concerned is supported by palaeontological evidence. The morphotype D- is typical of the living species of the genus *Martes* (Anderson, 1970; Rabeder, 1976; the present paper), which is presumably also true for the Lower and Middle Pleistocene *Martes vetus* Kretzoi, 1942 (Rabeder, 1976: Abb. 26, fig. 6), considered to be a probable ancestor of the subgenus *Martes* (Anderson, 1970). The two distinguished morphotypes of group E occurred in the Quaternary members of this genus (Rabeder, 1976; the present paper). A specimen of the Lower Pliocene *Martes wenzensis* Stach, 1959 (MF/342/60 Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Cracow), which may have been in the line of ancestry towards *M. vetus* (Anderson, 1970), shows the morphotypes Dc and E2. The morphotypes E1, E2, Da, Dc, Dac, and Dabc have been found in other Tertiary members of the genus *Martes s.l.*, with the latter two being the commonest of the group D (Gaillard, 1899; Viret, 1933; Dehm, 1950; Ginsburg, 1961, 1977; Petter, 1967a, 1971; Rabeder, 1976). The M^1 in the holotype specimen of the Lower Miocene *Paragale huerzeleri* Petter, 1967, one of the oldest known Mustelidae *s.s.* (Schmidt-Kittler, 1981), resembles the morphotype Dabcdef in morphology (Petter, 1967b; pl. 1, fig. 1d). The lingual portion of the tribosphenic upper molar in the late Cretaceous and early Cenozoic eutherian mammals consisted of a large central cusp (protocone) connected by two crests or ridges with antero-buccal and postero-buccal small cusps or cuspules (paraconule and metaconule, respectively) and sometimes of a postero-lingual cusp (hypocone). There was a short crest both between the paraconule and the anterior cingulum and between the metaconule and the posterior cingulum. The hypocone might have been united by a crest with the protocone and/or the posterior cingulum (Vandebroek, 1961). Thus, this pattern is very similar to that described for the E2 and non-D- morphotypes. Moreover, it is strikingly congruent with that extrapolated for the occlusal surface of the M^1 lingual lobe in *Martes* at an early stage in development preceding the threshold one. The ridge running postero-lingually from the medial portion of the anterior cingulum (Fig. 1, I), characteristic of the living species of *Martes*, would correspond to the anterior cingulum-paraconule-protocone crest of the tribosphenic upper molar, with the depression characteristic of the morphotype E2 being a counterpart of that separating the paraconule and protocone. The elevations developed along the buccal curve would conform with the protocone-metaconule-posterior cingulum crest, with the a, b, and c regions corresponding to the posterior protocone slope, the depression between the protocone and metaconule, and the metaconule with its posterior crest, respectively. Finally, the lingual curve with its d, e, and f regions would correspond to the protocone-hypocone-posterior cingulum crest with its anterior hypocone portion, hypocone, and posterior hypocone ridge, respectively (Fig. 1, II).

The complexity in the morphological pattern of the characters studied suggests that a group of genes rather than a single gene is responsible for their appearance. Therefore, a mutation necessary for the creation of this pattern would have to affect all the genes of the group, or more likely, several mutations following each other would be involved. It is obvious that the greater the number of mutations necessary for the creation of a structure, the less likely it is for the latter to originate twice independently in evolution.

The evidence adduced above indicates that the second of the explanations is much more probable than the first one. Thus, the characters under study would have never been genotypically lost in the course of evolution in the lineage of *Martes* during the Cenozoic. These characters seem to be of no functional and, consequently, adaptive importance in the living species of this genus. Hence, in all probability, they are no longer subject to the direct action of natural

Source : MNHN, Paris

selection. The above is presumably also true for many fossil members of the lineage, which explains the persistence of the involved genes in the lineage gene pool during such a long time. Therefore, the qualitative and quantitative differences discovered in the morphotype frequency distributions for the examined species and their populations would be due to genetic drift. It is also not out of the question that some pleiotropic genes selected for their non-dental effects may be concerned. Of course, the characters studied, non-adaptative now, remain of potential adaptiveness and may give a selective advantage in favourable circumstances. Perhaps the considerable extension of the occlusal surface of the M^1 lingual lobe in *Martes* facilitates their appearance.

As evidenced above, there is a general trend to simplification in the morphological pattern of the occlusal surface of the M^1 lingual portion in the lineage of *Martes*. According to this view, the morphotypes D- and E1 are the most progressive. Both the paleontological evidence, and the morphotype (Figs. 2 and 4) and enamel elevation (Fig. 3) frequency distributions for the living species of *Martes*, allow the reconstruction of the pattern of this simplification. And so, first of all, the protocone-hypocone-posterior cingulum crest would be subject to progressive simplification in shape and to simultaneous reduction in size, and subsequent loss. At first the posterior hypocone crest would be lost while the hypocone would remain for the longest time. The anterior cingulum-paraconule-protocone-metaconule-posterior cingulum crest would be involved next, with the posterior protocone portion being much more strongly affected. As concerns this portion, the metaconule would be the longest persisting, whereas the b region would disappear first and foremost. Anterior to the a region, the crest has only undergone shape simplification and size reduction, often resulting in the vanishing of the depression separating the paraconule and protocone.

To conclude, the minor variations in the morphology of the occlusal surface of the M^1 lingual lobe studied in the living species of the genus *Martes* elucidate the evolution of M^1 in its lineage, throwing light on the ancestry of the genus. More comprehensive population studies may contribute to an understanding of speciation in this genus.

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Absolute frequency distributions of bilateral and unilateral occurrences of the morphotypes of group D. Percentage frequencies of the unilateral occurrences are given in parentheses. N and n indicate numbers of scored teeth and skulls, respectively.

Morphotype	Occurrence		Occurrence	
	bilateral	unilateral (%)	bilateral	unilateral (%)
	M. zibellina ($n = \frac{1}{2} N = 676$)		*M. zibellina* × *M. martes* ($n = \frac{1}{2} N = 33$)	
D-	451	73 (13.9)	26	4 (13.3)
Da	2	13 (86.7)	—	—
Db	—	—	—	—
Dc	14	11 (44.0)	1	3 (75.0)
Dab	—	1 (100.0)	—	—
Dac	1	— (0)	—	—
Dbc	—	1 (100.0)	—	—
Dabc	—	2 (100.0)	1	— (0)
Dd	5	13 (72.2)	—	—
De	89	49 (35.5)	—	1 (100.0)
Dde	2	14 (87.5)	—	1 (100.0)
Dad	—	4 (100.0)	—	—
Dae	—	1 (100.0)	—	—
Dce	10	12 (54.5)	—	1 (100.0)
Dabce	1	1 (50.0)	—	—
Dcde	1	2 (66.7)	—	—
Dacde	—	1 (100.0)	—	—
Dabcde	—	2 (100.0)	—	—

Morphotype	Occurrence		Occurrence	
	bilateral	unilateral (%)	bilateral	unilateral (%)
	M. martes ($n = \frac{1}{2} N = 465$)		*M. americana* ($n = \frac{1}{2} N = 25$)	
D-	381	48 (11.2)	23	2 (8.0)
Da	7	28 (80.0)	—	—
Db	1	4 (80.0)	—	—
Dc	12	18 (60.0)	—	2 (100.0)
Dab	—	1 (100.0)	—	—
Dac	1	1 (50.0)	—	—
Dbc	—	2 (100.0)	—	—
Dabc	2	15 (88.2)	—	—
Dd	—	5 (100.0)	—	—
	M. foina ($n = \frac{1}{2} N = 186$)		*M. flavigula* ($n = \frac{1}{2} N = 40$)	
D-	129	15 (10.4)	39	1 (2.5)
Da	2	— (0)	—	—
Db	—	—	—	—
Dc	38	14 (26.9)	—	1 (100.0)
Dab	—	—	—	—
Dac	1	— (0)	—	—
Dbc	—	—	—	—
Dabc	—	—	—	—
Dd	1	1 (50.0)	—	—

TABLE 2. Absolute frequency distributions of bilateral and unilateral occurrences of the enamel elevations a, b, c, d, e, and f. Percentage frequencies of the unilateral occurrences are given in parentheses.

Elevation	Occurrence		Occurrence	
	bilateral	unilateral (%)	bilateral	unilateral (%)
	M. zibellina		*M. zibellina* × *M. martes*	
a	4	25 (86.2)	1	— (0)
b	1	7 (87.5)	1	— (0)
c	27	32 (54.2)	2	4 (66.7)
d	8	36 (81.8)	—	1 (100.0)
e	103	82 (44.3)	—	3 (100.0)
f	—	—	—	—
	M. martes		*M. americana*	
a	10	45 (81.8)	—	—
b	3	22 (88.0)	—	—
c	15	36 (70.6)	—	2 (100.0)
d	—	5 (100.0)	—	—
e	—	—	—	—
f	—	—	—	—
	M. foina		*M. flavigula*	
a	3	— (0)	—	—
b	—	—	—	—
c	39	14 (26.4)	—	1 (100.0)
d	1	1 (50.0)	—	—
e	—	—	—	—
f	—	—	—	—

Source : MNHN, Paris

TABLE 3. Absolute frequency distributions of bilateral and unilateral occurrences of the morphotypes of group E. Percentage frequencies of the unilateral occurrences are given in parentheses. N and n indicate numbers of scored teeth and skulls, respectively.

Population ($n = \frac{1}{2} N$)	Morphotype	Occurrence	
		bilateral	unilateral (%)
Martes zibellina			
Ural Mts. region (124)	E1	6	6 (50.0)
	E2	112	6 (5.1)
Central Asia (203)	E1	38	25 (39.7)
	E2	140	25 (15.2)
Far East (47)	E1	4	10 (71.4)
	E2	33	10 (23.3)
Kamchatka (281)	E1	34	31 (47.7)
	E2	216	31 (12.6)
Total (655)	E1	82	72 (46.8)
	E2	501	72 (12.6)
Martes zibellina × *Martes martes*			
Ural Mts. region (30)	E1	12	0 (0)
	E2	18	0 (0)
Martes martes			
Poland (141)	E1	7	9 (56.3)
	E2	125	9 (6.7)
Ukraine (16)	E1	4	1 (20.0)
	E2	11	1 (8.3)
Central part of European U.S.S.R. (39)	E1	8	5 (38.5)
	E2	26	5 (16.1)
Northern part of European U.S.S.R. (110)	E1	15	18 (54.5)
	E2	77	18 (18.9)
Caucasus Mts. region (74)	E1	17	11 (39.3)
	E2	46	11 (19.3)
Ural Mts. region (7)	E1	6	0 (0)
	E2	1	0 (0)
Total (387)	E1	57	44 (43.6)
	E2	286	44 (13.3)

Population ($n = \frac{1}{2} N$)	Morphotype	Occurrence	
		bilateral	unilateral (%)
Martes americana			
North America (25)	E1	24	0 (0)
	E2	1	0 (0)
Martes foina			
Poland (35)	E1	20	9 (31.0)
	E2	6	9 (60.0)
Ukraine (48)	E1	40	3 (7.0)
	E2	5	3 (37.5)
Caucasus Mts. region (75)	E1	16	13 (44.8)
	E2	46	13 (22.0)
Central Asia (13)	E1	6	3 (33.3)
	E2	4	3 (42.9)
Total (171)	E1	82	28 (25.5)
	E2	61	28 (31.5)
Martes flavigula			
Far East (39)	E1	33	1 (2.9)
	E2	5	1 (16.7)

Source : MNHN, Paris

Comparative Systematic Value Between Dental and External/Skeletal Features in Western European Chiroptera

P. SEVILLA & N. LOPEZ-MARTINEZ

ABSTRACT

Diagnostic characters in biosystematics have low variability and congruent distribution. In mammals they are mainly external and skeletal features. The distribution of diagnostic and non-diagnostic characters often shows a poor degree of congruence.

Dental characters of isolated teeth of 21 recent species of bats (Chiroptera) have been chosen and analyzed to compare with the distribution of external and skeletal diagnostic characters. The degree of congruence of these distributions would be a measure of the diagnostic value of dental characters.

A phenetic approach of the character analysis and clustering method (UPGMA and single linkage) and the correlation coefficient between the similarity matrices have been used for this purpose.

The classification based on dental features shows a higher power of discrimination and a lesser degree of stability than that based on the chosen external and skeletal features. Congruence between both sets of characters have been found to be one of the highest

RÉSUMÉ

Les caractères diagnostiques en biosystématique sont choisis pour leur faible variabilité et leur distribution concordante. Chez les Mammifères, ils se trouvent surtout dans la morphologie externe et le squelette. D'autres caractères sont considérés non-diagnostiques en raison de leur distribution peu concordante avec les caractères diagnostiques.

Dans 21 espèces récentes de chauve-souris (Chiroptères), nous avons choisi et analysé 23 caractères des dents isolées. La distribution de ces caractères dentaires dans les espèces étudiées est comparée avec la distribution des caractères diagnostiques de la morphologie externe et du squelette, sur lesquels est fondée l'identification de ces espèces. Le degré de concordance des deux distributions serait une mesure de la valeur diagnostique des caractères dentaires, qui pourraient alors être aussi utiles dans l'identification des espèces.

Les distributions des caractères ont été analysées par la méthode phénétique UPGMA et « single linkage », puis par l'analyse de corrélations entre les matrices de similitude.

La classification basée sur les caractères dentaires montre un plus grand pouvoir de discrimination que celle fondée sur les caractères externes et squelettiques, qui ne suffit pas à distinguer les 21 espèces. Elle a par contre un degré de stabilité plus faible, car les

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 255-266.

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Source : MNHN, Paris

(r = 0.77) and consequently, we conclude that dental characters in bats have a high diagnostic value and thus fossil and recent populations can be studied using the same criteria.

différentes méthodes arrivent à des groupements différents. La classification basée sur des caractères externes et squelettiques est plus stable, ne variant pas beaucoup quand on change la méthode de groupement.

La corrélation entre les deux matrices de similitude est l'une des plus grandes observées (0,77) ; on peut en conclure que les caractères dentaires chez les chauves-souris ont une distribution conforme avec celle des caractères diagnostiques, et donc peuvent être aussi utilisés en systématique. Par conséquent, les mêmes critères d'identification pourront être appliqués à l'étude des populations fossiles et récentes.

Introduction

Character analysis is the principal method in biosystematics, evolutionary biology, functional biology and other major branches of life sciences. The differentiation of taxa, which is the basis of all other biological and palaeontological studies, is itself based on selected diagnostic characters. A high systematic value is given to these characters because of their low variability and congruent distribution (they do not appear in every possible combination).

Biosystematics must analyze characters coming from a majority of sources: external morphology, dentition, skeletal and soft anatomy, karyological and molecular data. Congruence of character distributions obtained with diagnostic characters (mainly external and skeletal in vertebrates), and non-diagnostic features (either morphological, cytological or molecular) has been observed to be poor (Hemmer & Alcover, 1984; Luckett & Hartenberger, 1985; Sanchiz, 1985). It seems that there is no obvious overall pattern in character distribution.

In mammals, diagnostic characters of high value are mainly external and skeletal data (nose, ears, hair, tail, feet, dental formula and skull). Dental morphology of isolated teeth is rarely used as a source of diagnostic characters, and when so, at a low taxonomic level. On the contrary, dental morphology of isolated teeth is extensively used in palaeontology, and consequently, they constitute very important data for the reconstruction of evolutionary processes.

We attempt in this note to test the degree of congruence of the distribution of dental characters compared with the distribution of external and skeletal characters, using Chiroptera as a test case. The congruence among both distributions will be a measure of the diagnostic value of dental characters, as well as a test for the ability of palaeontologists to select valuable systematic characters in isolated teeth.

Material and method

We have selected twenty-one species of bats (nine genera included), which are the most common in Western Mediterranean Europe. Twenty-two external and skeletal morphological characters, and twenty-three dental ones were chosen from our observations and from the literature. For the dental characters, over fifty specimens of the most common species in Spain were studied. From other species which are more rarely found in Spain, such as *Tadarida teniotis, Barbastella barbastellus* and the three *Nyctalus*, only five specimens or under, were available for our study. We avoided using metric characters, commonly used in determining specimens because continuous variation does not allow objective division into discrete categories.

We do not deal in this note with phylogeny, but with character distribution. A phenetic approach would be the best procedure for studying the coherence of character distribution and the comparative congruence of classifications. The selected characters are figured (Figs. 1 and 2), and plotted in two "features × taxa" matrices (Tables I and II), one for external and skeletal

Source : MNHN, Paris

features and the other for dental features. Symbols used in the character tables have no evolutionary meaning.

The two similarity matrices were obtained using Jaccard index ($I = \frac{2c}{N1 + N2 - c}$). Each one has produced two phenograms by means of two different clustering methods: single linkage and UPGMA (Unweighted Pair Group Method using Arithmetic Average) (see Sneath & Sokal, 1973). Measurement of the agreement between the two similarity matrices was calculated by the product-moment correlation coefficient of Pearson, $rss = \frac{P}{\sigma_s \sigma_D}$ (Sneath & Sokal, 1973), which varies between 0 and 1; good correlations approach value 1.

A. *External and Skeletal Features*

1. *Nose-leaf:*
   — absent (0)
   — present (1)

2. *Narine openings:*
   — opening forwards (0)
   — opening upwards (1)

3. *Tragus:*
   — absent (O)
   — long and thin (1)
   — short and thin to moderately wide (2)

4. *Ears:*
   — big, widely extending over muzzle wben laid forward (0)
   — middle-sized, approximately ending at the muzzle when laid forward (1)
   — short, clearly not reaching the muzzle when laid forward (2)

5. *Ears:*
   — not joined at inner bases (0)
   — joined at inner bases (1)

6. *Antitragus:*
   — absent (0)
   — present (1)

7. *Number of mammary glands:*
   — one pair (0)
   — two pairs (1)

8. *Shape of wings:*
   — narrow (length 5th finger/length < 3rd finger 0.69) (0)
   — wide (length 5th finger/length > 3rd finger 0.70) (1)

9. *Tail:*
   — included in uropatagium, or at most, two vertebrae projecting from it (0)
   — conspicuously projecting fom uropatagium (1)

10. *Length of calcar:*
    — shorter than free border of interfemoral membrane (0)
    — approximately the same as free border of interfemoral membrane (1)
    — clearly longer than free border of interfemoral membrane (2)

11. *Epiblema:*
    — absent or rudimentary (0)
    — clearly present (1)

12. *Plagiopatagium joining the leg at:*
    — ankle (0)
    — base of outer toe (1)
    — middle of metatarsus (2)

13. *Premaxillaries:*
    — loosely joined to the skull (0)
    — fused to the skull (1)

14. *Secondary articulation of scapula:*
    — small (0)
    — middle-sized (1)
    — big (2)

15. *Distal tip of coracoid process:*
    — directed anteriorly (0)
    — directed posteriorly (1)

16. *Styloid process of humerus:*
    — long and sharp (0)
    — long and flat (1)
    — sbort and blunt (2)

17. *Second finger:*
    — without bony phalanx (0)
    — with one bony phalanx (1)

18. *Number of phalanges in third finger:*
    — two (0)
    — three (2)

19. *Second phalanx of third finger:*
    — twice or less than twice as long as the first one (0)
    — three times as long as the first one (1)

20. *Fibula:*
    — rudimentary (0)
    — well developed (1)

21. *Fibula articulating with:*
    — astragalus (0)
    — calcaneum (1)

22. *Feet phalanx formula:*
    — 2.2.2.2.2 (0)
    — 2.3.3.3.3 (1)

Source : MNHN, Paris

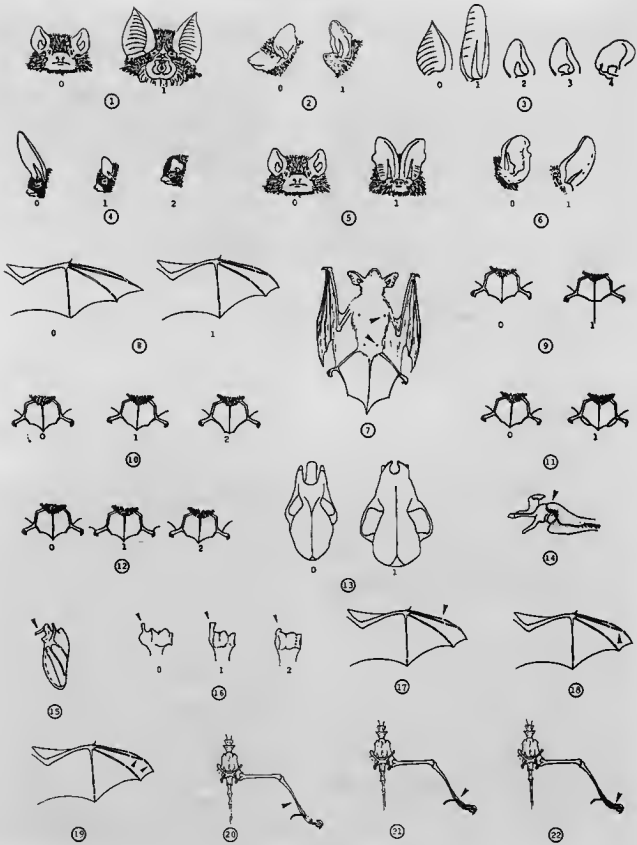

FIG. 1. — External and skeletal features. Explanation in the text.

Source : MNHN, Paris

Most of the morphological external features used for the determination of specimens were already described by Miller in 1907 and 1912. The shape of the wing has been calculated with Miller's data (1912). The presence of an extra pair of rudimentary mammary glands in *Rhinolophus* is described in Grassé (1948).

Many skeletal features also appear in Miller (1907, 1912), though some of them have been changed in our analysis according to more recent literature. This is the case, for example, of the presence of the fibula in the hind legs: according to Miller (1907) Rhinolophidae, Vespertilionidae and Molossidae present a complete fibula, whereas Dobson (1878), Flower (1885) and Flower & Lydekker (1891) describe it as incomplete in all Chiroptera except Molossidae. This fact has been recently checked by Walton & Walton (1970). These last authors are also the source of our character n. 21. On the other hand, character n. 14 has been preserved as found in Miller (1912), on the basis of personal observations. We do not agree with the data found in Walton & Walton for character n. 15, which has been included for the species of which we had material available. Character n. 15 corresponds to the three major groups in which the humera of European Chiroptera have been divided by Felten *et al.* (1973). The source of character n. 22 was Grassé (1948).

The matrix built with these characters can be observed in Table I.

B. *Dental Features*

1. *Number of cusps in* I^1*:*
   — one, very small (0)
   — one, well developed (1)
   — two (2)
   — three (3)

2. *Number of cusps in* I^2*:*
   — this tooth is absent (0)
   — one cusp (1)
   — two cusps (2)
   — three cusps (3)

3. *Number of cusps in* I_1*:*
   — two (1)
   — three (1)
   — four (2)

4. *Number of cusps in* I_2*:*
   — two (0)
   — three (1)
   — four (2)

5. *Number of cusps in* I_3*:*
   — this tooth is absent (0)
   — two (1)
   — three (2)
   — four (3)

6. *Number of grooves in upper C:*
   — none (0)
   — one, on the labial face (1)
   — two, one on the labial face, one on the lingual face (2)
   — three, one on the labial face, two on the lingual face (3)
   — four, two on each face (4)

7. *Cingular cusplet at mesiolingual margin of lower C:*
   — absent (0)
   — present (1)

8. *Number of upper premolars:*
   — one, P^4 (0)
   — two, P^2 being single-rooted (1)
   — three, P^2 and P^3 being single-rooted (2)
   — three, P^2 is single-rooted, P^3 with three roots (3)

9. *Cingular cusplet at mesiolingual margin of* P^4*:*
   — absent (0)
   — present (1)

10. *Number of lower premolars:*
    — two, P_2 is single-rooted (0)
    — three, P_2 and P_3 are single-rooted (1)
    — three, P_2 is single-rooted, P_3 is two-rooted (2)

11. *Cingulum of* P_4 *at labial view:*
    — straight and very oblique (0)
    — concave towards the roots (1)
    — with two concavities, each towards a root (2)

12. *Upper molars:*
    — without paraloph (0)
    — with paraloph (1)

13. *Two first upper molars:*
    — without heel (0)
    — with heel, but without hypocone (1)
    — with both heel and hypocone (2)

14. *Two first upper molars:*
    — without metaloph (0)
    — with metaloph (1)

15. *Two first upper molars:*
    — without metaconule (0)
    — with metaconule (1)

16. *Distal reduction of* M^3*:*
    — minimal, affecting almost exclusively the postmetacrista (0)

Source : MNHN, Paris

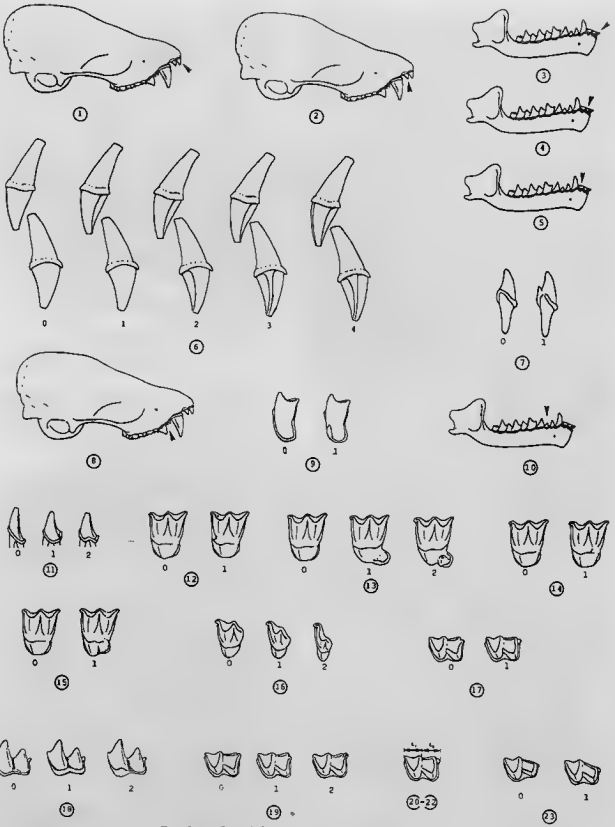

FIG. 2. — Dental features. Explanation in the text.

Source : MNHN, Paris

— intermediate, postparacrista and premetacrista somewhat reduced (1)
— very strong, postparacrista and premetacrista strongly reduced (2)

17. *Pattern of lower molars:*
— nyctalodont (0)
— myotodont (1)

18. *Thickness of labial cingulum in lower molars:*
— thin (max. height cingulum/length tooth < 0.09) (0)
— thick (max. height cingulum/length tooth > 0.12) (1)
— thick at trigonid, thin at the talonid (2)

19. *Base of hypoconulid in* M_1 *and* M_2*:*
— in line with the entoconid (0)
— more labial than the entoconid (1)
— more lingual than the entoconid (2)

20. *Trigonid of* M_1*:*
— open (length trigonid > length talonid (0)
— regular (length trigonid ≃ length talonid) (1)
— closed (length trigonid < length talonid) (2)

21. *Trigonid of* M_2*:*
(as n. 20)

22. *Trigonid of* M_3*:*
(as n. 20)

23. *Relative location of hypoconid in* M_3*:*
— clearly more labial than in M_2 (0)
— about the same as in M_2 (1)

The terminology used for the dental characters is after Van Valen (1966) and posterior modifications found in de Bruijn & Rümke (1974). In the systematics of recent bats, only dental formulae have been taken into account. In Miller (1907, 1912) some characters of the tooth morphology in bats are described, such as the presence of a heel in the upper molars, the presence of a hypocone (n. 13), and the metaconule, which he refers to as a hypocone (n. 15); the "secondary commissures", which are the paraloph (n. 12) and the metaloph (n. 14).

Palaeontologists have occasionally mentioned other characters (ns. 6, 19, 20, 21, 22, 23) in the description of fossil material, though no formal definition of features is found in the literature. For example, the openness of the trigonid in lower molars is sometimes mentioned, but no criterium to define "open" or "closed" is given.

We have added three new characters (ns. 11, 16, 18), as we consider them of systematic importance.

Results

The similarity matrices obtained with the Jaccard index are shown in Table III; the left half belongs to the external and skeletal features and the right half of the table belongs to the dental features. From each matrix we have obtained two different phenograms shown in Figs. 3 and 4, using single and average linkage. The four classifications are not identical, and we shall compare the congruence between them, and with the actual systematic arrangement.

Classifications based on external and skeletal features show a more constant pattern, with three main groups: Rhinolophidae, Molossidae and Vespertilionidae, with the first one quite distant from the two others. According to these arrangements, there is no reason for a Miniopteridae family group, as has been proposed by Mein & Tupinier (1977). The character pattern distribution is very coherent, and many diagnostic characters (ns. 1, 3, 10, 12, 13, 14, 16, 17, 18, 21, 22) can be retained. However, the level of specific differentiation is very poor, most of the species being morphologically identical. Absolute metric data are necessary to distinguish them.

Classifications based on dental features show a higher power of discrimination. Most of the species can be separated with a single morphologic dental character without using absolute metric data. The two families Rhinolophidae and Vespertilionidae appear clearly in both clusters, very far from one another. The Molossidae are also well characterized by dental features, but its position changes in both clusters. Miniopteridae appear as an independent taxon at the same level of differentiation as Molossidae. This taxon has been proposed on the basis of a heterogeneous set of characters (number of upper premolars, type of flight, reproductory physiology); the morphology of isolated teeth confirms its differences from the Vespertilionidae. The pattern of distribution of dental characters is less coherent than in the other case and consequently, the two classifications vary in a higher degree. However, diagnostic characters with high systematic value can be retained from our study (ns. 1, 5, 13, 16, 18).

Source : MNHN, Paris

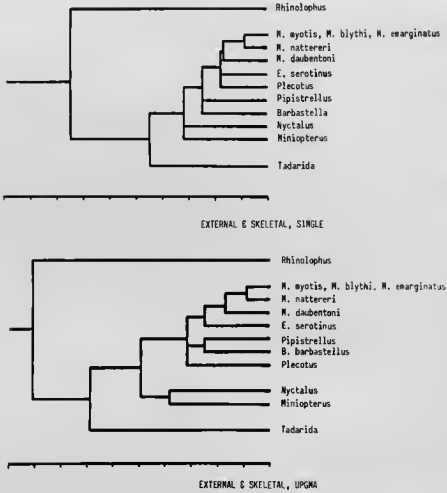

FIG. 3. — Single linkage and UPGMA clusters obtained with the external and skeletal features.

Congruence between classifications based on different sets of characters can be measured by correlating the two similarity matrices. The Pearson coefficient of correlation, r, is a good estimate of the degree of correspondence between the character distributions. In our case, r reaches a value of 0.77, which can be considered as a good agreement between both distributions. In Table IV, several correlations of two sets of characters in different groups can be compared with our results.

CONCLUSION

The comparative study of character distributions of external and skeletal vs. dental morphology in Chiroptera shows a good correlation between botb classifications. Dental features are better for the identification of species than external and skeletal features. Half of the external characters and one quarter of the dental ones show a high systematic value, appearing as diagnostic characters in the main clusters. The good agreement between both kinds of characters allows one to compare the results of studies of fossil and recent species of Chiroptera, and is a proof of the ability of the palaeontologists in selecting valid systematic characters in isolated teeth.

ACKNOWLEDGEMENTS

Our thanks to Miss C. Carrascosa, who processed our data.

Source : MNHN, Paris

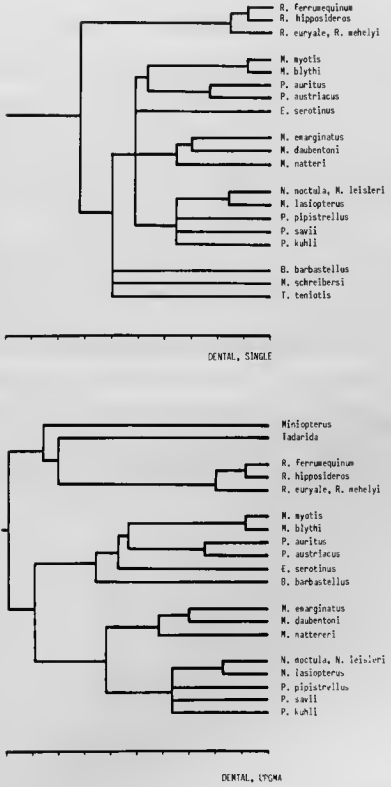

FIG. 4. — Single linkage and UPGMA clusters obtained with the dental features.

Source : MNHN, Paris

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Source : MNHN, Paris

TABLE I. Distribution in the different species of the external and skeletal features.

EXTERNAL AND SKELETAL FEATURES

SPECIES	Nose		Ears				M.g.	Patagium						S	Scap.		Arm					H. limbs		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Rhinolophus ferrumequinum	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus mehelyi	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus euryale	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus hipposideros	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Myotis myotis	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis blythi	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis emarginatus	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis nattereri	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis daubentoni	0	0	1	1	0	1	0	1	0	2	0	2	1	1	1	2	1	1	0	0	0	1
Pipistrellus pipistrellus	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Pipistrellus kuhli	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Pipistrellus savii	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Eptesicus serotinus	0	0	2	2	0	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Nyctalus noctula	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Nyctalus lasiopterus	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Nyctalus leisleri	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Barbastella barbastellus	0	1	1	1	1	0	0	1	0	1	1	1	1	1	—	2	1	1	0	0	0	1
Plecotus auritus	0	1	1	0	1	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Plecotus austriacus	0	1	1	0	1	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Miniopterus schreibersi	0	0	2	2	0	1	0	0	0	1	0	0	1	1	0	2	1	1	1	0	0	1
Tadarida teniotis	0	0	4	0	1	1	0	1	0	1	0	0	1	2	0	1	1	1	—	1	0	1

TABLE II. Distribution in the different species of the dental characters.

DENTAL FEATURES

SPECIES	Incisors					C		Premolars					Upper molars									Lower molars			
	1	2	3	4	5	6	7	8	9	10	11	12	12	13	14	15	16	17	18	19		20	21	22	23
Rhinolophus ferrumequinum	0	0	1	1	0	1	0	1	0	1	2		0	1	0	0	0	0	0	1		0	0	0	1
Rhinolophus mehelyi	0	0	1	1	0	0	0	1	1	1	2		0	1	0	0	0	0	0	1		0	0	0	1
Rhinolophus euryale	0	0	1	1	0	0	0	1	1	1	2		0	1	0	0	0	0	0	1		0	0	0	1
Rhinolophus hipposideros	0	0	1	1	0	1	0	1	0	1	2		0	1	0	0	0	0	0	1		0	0	1	1
Myotis myotis	3	3	2	2	3	2	0	2	0	1	2		0	0	0	0	2	1	2	0		1	1	0	0
Myotis blythi	3	3	2	2	3	2	0	2	0	1	2		0	0	0	0	2	1	2	0		1	1	1	0
Myotis emarginatus	3	3	2	2	3	2	1	2	0	1	2		1	0	1	1	1	1	2	0		2	2	2	0
Myotis nattereri	3	3	2	2	3	1	1	2	0	1	1		0	0	0	1	1	1	2	1		1	2	2	0
Myotis daubentoni	3	3	2	2	3	3	1	2	1	1	1		1	0	1	1	1	0	2	2		2	2	2	1
Pipistrellus pipistrellus	2	3	2	1	3	1	1	1	1	0	1		1	0	0	1	1	0	2	2		2	2	2	1
Pipistrellus kuhli	2	3	2	1	3	1	1	1	0	0	0		1	0	1	1	2	0	2	2		2	2	2	0
Pipistrellus savii	2	3	2	1	3	1	1	1	1	0	0		0	0	0	1	1	1	2	0		2	2	2	0
Eptesicus serotinus	2	2	2	2	3	3	1	0	1	0	2		2	0	0	0	2	1	2	0		0	1	0	0
Nyctalus noctula	2	2	2	2	3	0	1	1	1	0	0		1	0	1	1	1	0	2	0		2	2	2	1
Nyctalus lasiopterus	2	2	2	2	3	1	1	1	1	0	0		1	0	1	1	1	0	2	1		2	2	2	1
Nyctalus leisleri	2	2	2	2	3	0	1	1	1	0	0		1	0	1	1	1	0	2	0		2	2	2	1
Barbastella barbastellus	2	3	2	2	3	2	1	1	0	0	1		0	0	0	0	1	0	1	2		0	0	0	0
Plecotus auritus	2	2	1	2	3	2	1	1	0	1	2		0	0	0	0	2	1	2	2		1	2	2	0
Plecotus austriacus	2	2	1	2	3	2	1	1	0	1	2		0	0	0	0	2	1	2	0		0	2	1	0
Miniopterus schreibersi	2	1	1	2	2	4	1	3	1	2	0		1	1	1	1	1	0	1	1		0	2	1	1
Tadarida teniotis	*1*	*0*	*0*	*0*	*1*	*0*	*0*	*1*	*1*	*0*	*1*		*1*	*2*	*0*	*0*	*1*	*1*	*0*	*2*	*1*	*2*	*2*	*2*	*1*

Source : MNHN, Paris

TABLE III. Similarity matrices. Upper right, dental characters; lower left, external and skeletal.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	—	84.0	84.0	91.7	21.1	17.9	7.0	15.0	4.5	15.0	12.2	12.2	12.2	7.0	12.2	7.0	24.3	21.1	24.3	15.0	21.1
2	100	—	100	76.9	17.9	15.0	4.5	9.5	7.0	15.0	7.0	12.2	15.0	12.2	12.2	12.2	21.1	17.9	21.1	17.9	27.8
3	100	100	—	76.9	17.9	15.0	4.5	9.5	7.0	15.0	7.0	12.2	15.0	12.2	12.2	12.2	21.1	17.9	21.1	17.9	27.8
4	100	100	100	—	17.9	21.1	7.0	15.0	4.5	15.0	12.2	12.2	9.5	7.0	12.2	7.0	21.1	21.1	27.8	17.9	21.1
5	25.0	25.0	25.0	25.0	—	91.7	48.4	48.4	31.4	15.0	21.1	27.8	43.8	15.0	12.2	15.0	35.3	48.4	48.4	2.2	9.5
6	25.0	25.0	25.0	25.0	100	—	48.4	48.4	31.4	15.0	21.1	27.8	39.4	15.0	12.2	15.0	31.4	48.4	53.3	4.5	9.5
7	25.0	25.0	25.0	25.0	100	100	—	58.6	70.4	35.3	43.8	43.8	31.4	43.8	39.4	43.8	27.8	39.4	39.4	17.9	15.0
8	21.2	21.2	21.2	21.2	91.3	91.3	91.3	—	64.3	39.4	35.3	48.4	31.4	27.8	35.3	27.8	35.3	43.8	35.3	15.0	17.9
9	25.0	25.0	25.0	25.0	83.3	83.3	83.3	76.0	—	43.8	39.4	43.8	31.4	43.8	48.4	43.8	24.3	27.8	24.3	24.3	24.3
10	17.6	17.6	17.6	17.6	69.2	69.2	69.2	63.0	69.2	—	64.3	64.3	27.8	58.6	64.3	58.6	39.4	27.8	21.1	24.3	39.4
11	17.9	17.9	17.9	17.9	69.2	69.2	69.2	63.0	69.2	100	—	58.6	27.8	53.3	58.6	53.3	35.3	35.3	27.8	21.1	21.1
12	17.6	17.6	17.6	17.6	69.2	69.2	69.2	63.0	69.2	100	100	—	43.8	53.3	53.3	53.3	35.3	35.3	35.3	17.9	24.3
13	18.8	18.8	18.8	18.8	82.6	82.6	82.6	82.6	68.0	75.0	75.0	75.0	—	35.3	31.4	35.3	35.3	39.4	48.4	15.0	9.5
14	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	—	84.0	100	27.8	27.8	27.8	35.3	35.3
15	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	100	—	84.0	27.8	27.8	24.3	39.4	35.3
16	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	100	100	—	27.8	27.8	27.8	35.3	35.3
17	11.8	11.8	11.8	11.8	68.0	68.0	68.0	61.5	55.6	61.5	61.5	61.5	55.6	50.0	50.0	50.0	—	39.4	39.4	17.9	17.9
18	15.2	15.2	15.2	15.2	75.0	75.0	75.0	82.6	61.5	55.6	55.6	55.6	68.0	50.0	50.0	50.0	75.0	—	76.9	12.2	15.0
19	15.2	15.2	15.2	15.2	75.0	75.0	75.0	82.6	61.5	55.6	55.6	55.6	68.0	50.0	50.0	50.0	75.0	100	—	17.9	12.2
20	17.6	17.6	17.6	17.6	51.7	51.7	51.7	51.7	46.7	51.7	51.7	51.7	68.0	68.0	68.0	68.0	35.5	44.8	44.8	—	17.9
21	8.1	8.1	8.1	8.1	35.5	35.5	35.5	40.0	31.3	31.3	31.3	31.3	37.9	42.9	42.9	42.9	29.0	42.9	42.9	55.6	—

TABLE IV. Comparative results of studies on congruence of characters between different sets of characters (Sneath & Sokal, 1973). The high value of correlation obtained between the two sets of characters in Chiroptera means that the grouping obtained with the external and skeletal features used in the current systematics is highly similar to that obtained with the chosen dental characters. The use of these for the identification of dental remains is, thus, highly justified.

Group of organisms	Sets of characters	N of characters	Value of r
Angiosperm	Floral/Vegetative	61/32	0.17
Bees	Head/the rest	60/62	0.61
Butterflies	External/Internal	100/96	0.69
Birds	Wing/Leg External/Skeletal	82/93 72/51	0.62 0.73
Chiroptera	Extern. & Skelet. Dental	22/23	0.77

Source : MNHN, Paris

Particularités Morphologiques d'une Molaire de Mammifère Créodonte : Interprétation Fonctionnelle

B. LANGE-BADRÉ

ABSTRACT

The morphology of a lower molar attributed to a new Palaeonictinae Creodont, *Dormaalodon woutersi* Lange-Badré is described. The morphologic particularities, notably the complete separation of the metaconid from the trigonid and its participation in the formation of a " well "-shaped talonid, are interpreted.

Clearly delimited wear facets permit the proposal of a structural model for the upper molars in occlusal position. Examination of these facets by scanning electron microscope brought out phenomena of relief engendered by the rubbing of food during mastication; from their orientation, a hypothesis is proposed concerning an unusual mechanism, for a carnivorous mammal, of food laceration, that is, by pinching and pulling.

RÉSUMÉ

La morphologie d'une molaire inférieure rapportée à un nouveau Créodonte Paléonictiné, *Dormaalodon woutersi* Lange-Badré, est décrite. Les particularités morphologiques, notamment la complète séparation du métaconide du trigonide et sa participation á la formation d'un talonide en « puits », sont interprétées d'un point de vue fonctionnel.

Les facettes d'usure nettement délimitées permettent de proposer un modèle structural pour les molaires supérieures venant en occlusion. L'examen de ces facettes au M.E.B. a mis en évidence les reliefs engendrés par le frottement des aliments au cours de la mastication ; d'après leur orientation, il est proposé une hypothèse concernant un mécanisme original de lacération des aliments pour un mammifère carnassier, par pincement et étirement.

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Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

Dans le matériel provenant du gisement de Dormaal (base de l'Éocène, Belgique) et ayant pu appartenir à des mammifères placentaires, a été découverte une molaire inférieure présentant une morphologie tout à fait inhabituelle, et attribuée à un Créodonte Paléonictiné nouveau, *Dormaalodon woutersi* Lange-Badré 1987.

Observations

Il s'agit d'une molaire droite, brachyodonte, de petite taille (8,2 × 5,4 mm), ayant appartenu à un individu adulte. Les différences de hauteur et de largeur permettent d'identifier aisément les deux parties fondamentales d'une molaire tribosphénique inférieure : le trigonide et le talonide (Fig. 1a et b).

Trigonide. — Le paraconide et le protoconide, presque d'égale longueur vestibulaire, forment une muraille oblique, faisant un angle d'environ 60° par rapport à l'axe antéro-postérieur de la dent. A peine peut-on qualifier cet ensemble de lame, tant il est épais et robuste. La face mésiale du paraconide porte les vestiges de l'ectocingulum, redressés à la verticale. En raison de la forte abrasion des deux cuspides, le paraconide et le protoconide sont de même hauteur. Mais le protoconide n'a jamais dû être beaucoup plus élevé que le paraconide.

Sur la face linguale, en contrebas et nettement en arrière du protoconide, se détache une cuspide trapue, de forme équilatérale et d'une hauteur égale à la moitié environ de celle du protoconide. Selon toute évidence, il s'agit du métaconide dont les relations avec les autres cuspides de la dent sont particulières et inhabituelles. Ce métaconide est d'une part totalement dissocié des deux autres cuspides du trigonide, sans aucune connexion avec le protoconide dont un large sillon le sépare, d'autre part il a contracté une double liaison vestibulaire et linguale avec le talonide (Fig. 1c).

L'isolement mésial du métaconide procède du recul de celui-ci, combiné à l'approfondissement et à l'élargissement du sillon entre métaconide et protoconide [sillon intraépicristide, selon Hershkovitz (1971) ou sillon intraprotolophide, d'après Van Valen (1966)]. Une large gouttière fait alors communiquer le bassin du trigonide avec la face vestibulaire sur laquelle elle débouche à la limite du talonide, au niveau de l'ectoflexide (Fig. 1a et c). Cependant on peut considérer que la relation avec le trigonide est partiellement maintenue, mais de façon ténue, par l'intermédiaire d'un cingulum lingual bien développé et continu, reliant la base du métaconide à celle du paraconide (Fig. 1b).

Fig. 1. — Molaire inférieure (M_1) de *Dormaalodon woutersi* Lange-Badré 1987 : a, face vestibulaire. b, face linguale. c, face occlusale. × 4 environ.
Clichés a et b, Institut de Paléontologie, MNHN, Paris ; c, IRSN, Bruxelles.

Talonide. — Le talonide revêt lui aussi un aspect inhabituel pour une molaire tribosphénique (Fig. 1c). Le bassin est en forme de puits étroit et profond, allongé vestibulo-lingualement. Il est dominé par deux cuspides diamétralement opposées, l'une linguale, le métaconide, l'autre vestibulo-distale, probablement l'hypoconide, à moins qu'il s'agisse de l'hypoconulide et de l'hypoconide fusionnés. Il n'y a aucune trace d'entoconide. Le bord du talonide entre le métaconide et le supposé hypoconide est continu et haut mais il est profondément échancré sur les deux faces linguale et buccale.

Par rapport au schéma tribosphénique ancestral, cette molaire inférieure présente donc d'importantes différences. Avant d'envisager les conséquences de ces variations sur le plan fonctionnel, nous examinerons l'autre aspect morphologique que sont les traces d'usure dont l'apparition est

Source : MNHN, Paris

consécutive à l'affrontement des reliefs dentaires et du frottement de la nourriture au cours de sa fragmentation, car ce sont lá les témoins des corrélations entre la forme et la fonction des dents.

Usure. — Des traces d'usure s'observent sur deux zones bien délimitées de la face vestibulaire (Fig. 2). L'une, antérieure, couvre le paraconide et le protoconide, l'autre, distale, le talonide. Elles présentent toutes les deux, une certaine obliquité mésio-linguale — disto-vestibulaire, la facette antérieure étant plus inclinée que la distale, par rapport á l'axe antéro-postérieur de la dent.

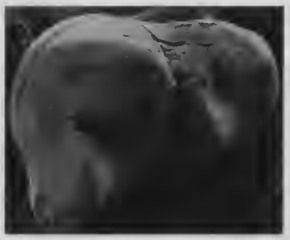

FIG. 2. — Facettes d'usure de la molaire inférieure de *D. woutersi* L.-B.
Cliché MEB, IRSN, Bruxelles. × 8,5 environ.

La surface d'usure couvrant le paraconide et le protoconide — la plus grande des deux — est d'abord convexe au voisinage du sommet des deux cuspides, puis légérement concave. L'émail est abrasé jusqu'au tiers inférieur de la couronne. La dentine ainsi mise á nu, est entourée d'une étroite auréole d'émail aminci et lissé. Entre dentine et émail, il n'y a pas de brusque dénivellation mais un passage progressif à peine marqué par un faible épaississement d'émail.

L'examen au microscope électronique á balayage (MEB) de cette zone (Pl. 1, A) montre l'existence de fines crêtes parallèles, peu écartées les unes des autres, séparées par des sillons plus larges, peu profonds et à fond plat. L'ensemble est allongé obliquement selon l'axe antéro-postérieur de la face mésio-vestibulaire du trigonide. A la limite inférieure de la facette d'usure, crêtes et sillons deviennent moins nombreux mais plus grands. Aucune différence de tracé ne marque le passage de l'émail á la dentine.

Les crêtes et les sillons sont des traces couramment observées sur les facettes d'usure dentaire (Rensberger, 1978). Ils n'ont pas de signification particulière. On peut simplement en déduire que le matériau á l'origine de ces marques était peu abrasif et peu dur.

Le bord mésial du paraconide, non loin du sommet (Fig. 2) est creusé d'une sorte de cupule, sans adjonction de crête ou de sillon, qui correspond sans doute á l'impact répété du protocône de la dent supérieure antagoniste, au moment de l'occlusion.

La seconde surface d'usure, portée par le talonide, est moins bien délimitée que la première. L'émail très altéré présente de nombreuses petites dépressions irrégulières, comme les autres faces de la dent, dues á la corrosion post-mortem.

La dentine est apparente au sommet et sur la face vestibulaire du métaconide, creusée en outre d'une courte gouttière, probablement par le passage du paracône de la dent supérieure opposée (Pl. 1, C). Au MEB, dans un étroit secteur à la base de l'hypoconide (Pl. 1, B), on observe des côtes épaisses, onduleuses, assez courtes, irrégulièrement espacées, plus ou moins parallèles et séparées par de larges sillons. La brièveté et l'irrégularité de ces reliefs suggérent qu'ils aient pris naissance par écrasement de particules alimentaires peu dures et arrondies. D'aprés leur localisation sur le bord et dans la partie moyenne de l'hypoconide, ces marques seraient consécutives á une pression dentaire accrue correspondant á la fin de la phase d'occlusion.

L'orientation des crêtes et des sillons sur la surface dentaire est le reflet de la direction des mouvements de la mandibule. Chez *D. woutersi*, ils s'exerçaient préférentiellement dans le sens symphyse-condyle comme chez la plupart des mammifères prédateurs, avec une composante verticale assez faible. Les différences relevées dans l'impression des reliefs observés sur les deux facettes d'usure sont peu importantes. Elles sont vraisemblablement dues aux variations de pressions exercées par les dents au cours des différentes phases de la mastication.

Enfin, sur la face distale du talonide, on relève des traces de frottements qui permettent de

Source : MNHN, Paris

préciser que cette molaire n'occupait pas la dernière place dans la rangée dentaire. Il s'agit donc soit d'une M_1, soit d'une M_2.

Discussion

La forme des dents des mammifères est la réponse adaptative au problème de la préparation des aliments dans la cavité buccale avant la déglutition (Lucas, 1979). En effet, il existe d'étroites relations entre la forme et la fonction des dents. D'un point de vue mécanique, les deux rangées dentaires supérieure et inférieure, fonctionnent comme un système unique et clos. Par conséquent, en présence de molaires d'une des deux rangées, il doit être possible de déduire les principales caractéristiques des dents antagonistes.

L'analyse des structures dentaires en terme d'occlusion et de mouvement des mâchoires a donné lieu à de nombreux travaux (Butler, 1961 ; Mills, 1966 ; Crompton & Hiemae, 1970 ; Crompton & Kielan-Jaworowska, 1978 ...), plutôt axés sur l'interprétation des molaires des mammifères mésozoïques. Cependant à partir des études faites sur les euthériens crétacés dont la disposition est considérée comme primitive, on peut essayer d'expliquer les différents modèles rencontrés chez les mammifères plus récents et d'interpréter les conséquences fonctionnelles des variations observées. C'est dans cette perspective que la morphologie et les facettes d'usure de la molaire inférieure de *D. woutersi* ont été comparées à celles de *Cimolestes incisivus* (Proteutheria, Palaeoryctidae).

D'après Crompton (1971) et Crompton & Kielan-Jaworowska (1978), la M_2 de *C. incisivus* comporte six surfaces coupantes et une extension postérieure (talonide) qui affronte une zone triangulaire supérieure (protocône) (Fig. 3). Les molaires de ce type sont particulièrement bien adaptées à la découpe et à la perforation des aliments. Les principales surfaces coupantes sont des surfaces subverticales du trigonide qui s'encastrent dans l'embrasure séparant deux dents supérieures successives. La surface 1a, entre protoconide et métaconide affronte la surface 1, formée par le stylocône, le paracône et le paraconule. La surface 2a, en avant du trigonide, rencontre successivement l'arrière du trigone de M^1, le métastyle et le métacône, en 2, puis le cingulum et l'aile postérieure du métaconule. La zone de coupe 3 est délimitée par les surfaces linguales du paracône et du paraconule. Dans l'embrasure en forme de V qui les sépare du métacône, vient prendre place la face vestibulaire, 3a, de l'hypoconide. Quant à la surface 4, elle correspond à la face linguale du métacône et au bord antérieur du métaconule qui entre en contact avec l'espace, 4a, entre l'hypoconide et l'hypoconulide. Enfin, le bord antérieur du protocône, 5, s'oppose à la face postérieure du métaconide, 5a, tandis que le bord postéro-lingual, 6, vient frotter contre la surface antéro-interne de l'hypoconulide et de l'entoconide 6a. Sur la face vestibulaire, le parastyle plus ou moins crochu, bloque le protoconide et empêche l'insertion de nourriture entre deux dents contigües. Dans le bassin du talonide, peu profond, s'emboîte un petit protocône pointu, empêchant tout mouvement vers le haut et le plan sagittal quand les dents sont en occlusion centrée.

Considérons à présent la molaire de *D. woutersi*. L'ambiguïté concernant la place occupée par cette dent dans la rangée dentaire (M_2 ou M_3) se trouve levée par le biais de sa détermination systématique puisqu'elle a été rapportée à un Paléonictiné. Or, tous les Paléonictinés connus jusqu'à présent, ont deux molaires inférieures (et supérieures), la deuxième inférieure étant morphologiquement très semblable à la première mais d'environ 20 % plus petite. Comme il a été dit précédemment que, d'après les facettes d'usure, cette molaire ne pouvait pas être la dernière de la rangée, il s'agit donc d'une M_1. A la fermeture des mâchoires, cette M_1 entrait en contact avec P^4 et M^1. En transposant les corrélations établies entre les surfaces appariées de *C. incisivus* lors de l'occlusion, il est alors possible de proposer une reconstitution au moins schématique de la P^4 et de la M^1 de *D. woutersi* (Fig. 4).

La surface 2a rencontrait le métastyle et le rebord distal du protocône (éventuellement la face distale de la base du paracône) de P^4. L'ensemble formait un angle d'environ 30° par rapport à l'axe antéro-postérieur de la prémolaire. Le métastyle était plutôt court, non rejeté vestibulairement, mais plus ou moins aligné sur le paracône.

Les autres surfaces de contact s'opposaient à

Source : MNHN, Paris

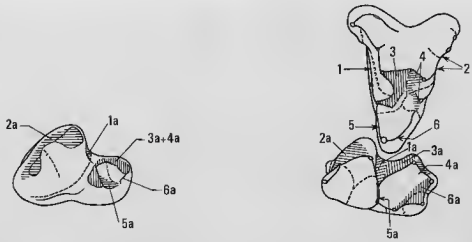

FIG. 3. — Interprétation des facettes d'usure de la molaire inférieure de *D. woutersi* L.-B., (à gauche) comparée à celles de la M_1 de *Cimolestes incisivus* figurée en occlusion avec la M^2 (à droite) (d'après Crompton & Kielan-Jaworowska, 1978). L'explication des symboles est dans le texte.

celles de M^1. La surface 1a, réduite á l'étroite face distale du protoconide, affrontait la zone raccourcie correspondant au stylocône, paracône et paraconule. On peut en déduire qu'il n'y avait probablement pas de stylocône et que le paracône était vertical, très proche à la fois du bord vestibulaire et de l'angle mésio-buccal de la dent. Quant au parastyle, il était peu développé, voire inexistant. La surface 3a est inhabituellement allongée, puisque la face vestibulaire du talonide prolonge celle du métaconide. La facette ainsi constituée, présente en outre une obliquité moins grande que celle de la surface 2a. Mais avant d'envisager l'antagoniste de la facette 3a, il convient d'examiner la surface 4a. La position particulière occupée par l'hypoconide à l'extrémité distale du talonide force à admettre que la surface 4a très réduite, n'avait guère de contact avec la M^1. La facette 4a aurait-elle disparu ? Bien que cela soit le cas chez les Tenrecidae et les Chrysochloridae (Mills, 1966), cela paraît a priori, peu probable dans la mesure où cette

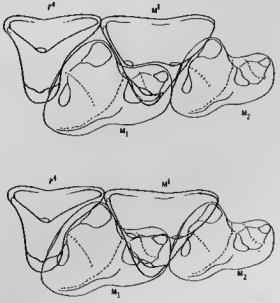

FIG. 4. — Reconstitution de l'occlusion des molaires de *D. woutersi* L.-B. Phase initiale, en haut ; phase finale, en bas.

Source : MNHN, Paris

facette correspond à la face antéro-linguale du métacône, mais un contact différent de celui de la molaire primitive a pu être réalisé. Il suffit pour cela que le sillon séparant habituellement le paracône du métacône ait disparu et que la face antéro-linguale du métacône se trouve dans le prolongement de celle du paracône, toutes deux étant fort convexes. Le métacône devait être moins volumineux que le paracône et le métastyle qui lui faisait suite, court, peut-être même non séparé par un sillon carnassier, du métacône.

A partir de la forme, de la profondeur et de l'orientation du bassin du talonide, on peut reconstituer les principaux traits du protocône de M^1. Il devait être étroit et allongé obliquement vestibulo-lingualement, assez proche de la base des cuspides vestibulaires et en position plus distale que mésiale. Sa hauteur était inférieure à la profondeur du bassin du talonide puisque le fond de ce dernier est dépourvu de trace de frottement. Il ne pouvait entrer en contact avec lui que lorsque le trigonide était déjà très abrasé.

Le rôle du métaconide est apparu en considérant les rapports entre les dents des deux rangées au cours de la morsure. Le métaconide et l'hypoconide encadraient le protocône qui, ayant emprunté l'échancrure les séparant, venait s'imbriquer dans le bassin du talonide, à l'occlusion centrée. Par sa position reculée, le métaconide jouait apparemment un double rôle : guider le protocône pendant la fermeture des mâchoires et empêcher tout mouvement vers l'avant et le haut à la fin de l'occlusion. Ainsi, l'ensemble métaconide et protocône faisait-il office de verrou. Sur les molaires tribosphéniques, cette fonction, nous l'avons vue, est accomplie par le duo parastyle-protoconide. Chez *D. woutersi*, il y a donc eu un glissement de fonction vers le métaconide et le protocône, en relation avec la régression du parastyle et la spécialisation carnassière du protoconide.

Disposant à présent d'un schéma assez précis de la P^4 et de la M^1 de *D. woutersi*, deux phases d'occlusion (début et fin ont été représentées (Fig. 4), mettant nettement en évidence les différences fonctionnelles entre *C. incisivus* et le spécimen belge. Par rapport à *C. incisivus*, *D. woutersi* a perdu le parastyle et l'entoconide. Le métacône est petit et dans son prolongement, la métacrista courte, n'était probablement pas individualisée par un sillon carnassier. Le protocône est reculé par rapport au paracône volumineux. La face vestibulaire du talonide participait activement à la fois à la découpe et au broyage des aliments.

A voir l'aspect des molaires de *C. incisivus* et de *D. woutersi*, il est évident que les dents des deux espèces travaillaient différemment, au cours de la mastication. Les molaires de *C. incisivus*, aux cuspides étroites et pointues et aux arêtes effilées étaient adaptées à un mode de vie carnassier (Crompton & Kielan-Jaworowska, 1978), mettant en œuvre la perforation et la coupe des aliments. *D. woutersi* avec ses molaires basses et épaisses, aux arêtes émoussées, découpait sa nourriture par compression et lacération. Contre la face mésio-vestibulaire, les aliments étaient d'abord coincés, puis découpés par pincement et étirement jusqu'à la limite de leur résistance mécanique. Le long du talonide, les particules ainsi détachées finissaient d'être écrasées.

Selon Osborn & Lumsden (1978), si les bords des plans de découpe ne se rencontrent pas, la nourriture est piégée entre les surfaces mais elle ne peut pas être coupée, à moins qu'un mouvement de bascule latérale de la mandibule ajuste les deux rangées dentaires l'une à l'autre comme dans le genre *Hyaenodon*. La symphyse mandibulaire non soudée que l'on observe chez de nombreux mammifères constitue un autre mécanisme adaptatif. Sous l'action des muscles ptérygoïdiens internes, le côté travaillant de la mandibule est mobilisé et le relief offert par la convexité de la face buccale des molaires inférieures est accru et renforce l'efficacité du mouvement de bascule.

Quant au sillon transversal faisant communiquer le bassin peu profond du trigonide avec la face buccale, et dont la présence semble liée au déplacement du métaconide, à notre avis, il joue un rôle particulier. N'appartenant pas à la surface occlusale, il n'a pas de contre-partie directe sur la dent supérieure, aussi est-il rarement mentionné dans les études fonctionnelles. Pourtant, il se rattache à l'ensemble des dépressions, formé par le bassin et les sillons périphériques s'y déversant (sillons intraparalophide et intraprotolophide). Des deux interprétations avancées par Crompton (1974) au sujet du sillon intraprotolophide des carnassières de carnivores et par Osborn & Lumsden (1978) pour les vallées séparant les cuspides des omnivores, ni l'une, ni l'autre ne convient ici. Il ne s'agit pas d'une structure maintenant les aliments au cours du

Source : MNHN, Paris

cisaillement, ni d'une sorte de miniréservoir dans lequel la nourriture est broyée. Ce sillon représente un élément du système d'évacuation des particules alimentaires, une fois détachées et écrasées par les molaires. Il assurait l'acheminement des aliments mastiqués et imprégnés de salive de la face buccale vers la face linguale. Là, le cingulum lingual, particulièrement développé, assurait le relais, en détournant et en canalisant le flux alimentaire vers l'avant de la cavité buccale, la langue et le palais, avant la phase de déglutition. Ce même cingulum peut aussi avoir joué un rôle protecteur du collet dentaire et de la gencive.

Cette interprétation fonctionnelle du cingulum lingual ne peut cependant être prise en compte que si *D. woutersi* avait une alimentation á base carnée ou particulièrement riche en aliments succulents. Or, la prépondérance du versant buccal sur le lingual comme chez les mammifères prédateurs très spécialisés, autorise à supposer un mode de vie carnassier á *D. woutersi*. On sait aussi que 40 á 60 % du poids du tissu musculaire consommé par un carnassier sont formés par l'eau de constitution. Si, à ce volume aqueux, on ajoute celui de la sécrétion salivaire très importante chez les consommateurs de protéines où la salive joue le rôle de stimulant des terminaisons gustatives et de diluant du pH, on aura un bol alimentaire de consistance particulièrement liquide pour laquelle *D. woutersi* aurait réalisé deux adaptations particulières : un sillon transversal intramolaire et un cingulum lingual entre le paraconide et le métaconide.

Conclusion

Ainsi, par le biais de l'étude morpho-fonctionnelle, les caractéres dérivés de la molaire inférieure de *D. woutersi*, peuvent-ils être interprétés, et une reconstitution des dents jugales supérieures venant en occlusion peut-elle être proposée.

Malgré l'absence des caractéres sectoriaux habituellement présents chez les mammifères prédateurs, tout porte à penser que *D. woutersi* était un carnassier. Mais, en l'absence de hautes cuspides pointues, d'arêtes aiguës et de tranchants affûtés, c'est par une technique différente de celle du couperet qu'il fragmentait sa nourriture. Celle-ci était constituée soit de proies de petite taille, soit de masses charnues, opposant peu de résistance á la dilacération.

Une fonction, aussi spécialisée apparemment que la coupe des aliments par les prédateurs, peut donc être réalisée de façon efficace, par la mise en œuvre de techniques variées. La diversité morphologique, expression concrète de l'adaptation fonctionnelle, est la réponse aux problémes biologiques et écologiques auxquels elle se trouve confrontée.

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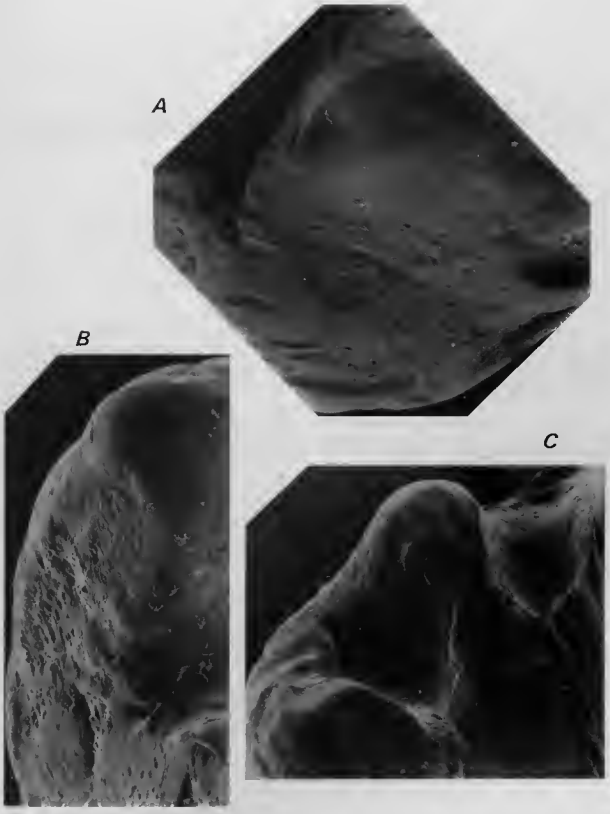

PL. I. — Microphotographies de la surface de la molaire inférieure de *D. woutersi* L.-B.
A, Face vestibulaire du paraconide. × 22,5.
B, Face vestibulaire et bord distal de l'hypoconide. × 30.
C, Vue occluso-vestibulaire du talonide. × 30.
Clichés MEB, IRSN, Bruxelles.

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Quelques Dents Fossiles de Morphologie Aberrante

P. MEIN

ABSTRACT

This article discusses some teeth with abnormal structures from small fossil mammals (Cricetidae, Sciuridae, Soricidae). Abnormal fossil teeth are always rare: those studied here are from the Miocene karstic fissures of La Grive Saint-Alban (Isère) that have yielded tens of thousands of specimens.

The anomalies met with vary from those that affect only a small part of the tooth, such as, lacking a cusp or having one too many, or a linking crest that is absent or one with an unexpected orientation; these could be considered as exceptional cases but still within the normal morphotype, although very rare. Other examples show very aberrant tooth parts, due either to aplasia or to doubling, adjacent to normal areas that suffice to correctly identify the tooth. Still other specimens are so greatly modified that the morphology is no longer recognizable. Another category concerns the last lower cheek tooth wherein the posterior portion is abnormally reduced: one may suppose this to represent a supernumerary tooth (M_4), an anomaly found in diverse living Eutherians (figured here is a mandible of *Sciurus vulgaris* in which an M_4 is bilaterally present). Other anomalies more difficult to interpret could result either from traumatisms affecting the germs during calcification, or from chromosomic variations. An interesting case is when a structure that is aberrant for a given genus becomes a constant character in related genera (the abnormal supplementary lingual cusp in *Megacricetodon* becoming frequent in the Myocricetodontinae, then constant (t4) in the Dendromurinae, Cricetomyinae and Murinae).

RÉSUMÉ

Cette note fait connaître quelques dents fossiles de petits mammifères à structure anormale (Cricetidae, Sciuridae, Soricidae). Les dents fossiles anormales sont toujours des raretés ; celles qui furent étudiées proviennent des fissures karstiques miocènes de la Grive Saint-Alban (Isère) qui ont livré des dizaines de milliers de spécimens.

Les anomalies rencontrées vont depuis celles qui n'affectent qu'une petite portion de la dent : une cuspide en plus ou en moins ou une crête de liaison absente ou au trajet imprévu et qui peuvent à la rigueur passer pour des morphotypes normaux bien que très rares. Nous rencontrons ensuite des dents présentant des portions très aberrantes soit par aplasie soit par dédoublement, adjacentes à des portions normales qui suffisent à déterminer correctement la dent. Ensuite des dents tellement modifiées que la morphologie n'est plus reconnaissable. Enfin une autre catégorie rencontrée concerne des dernières dents jugales inférieures dont la portion distale est anormalement réduite ; on peut dans ce cas supposer qu'il s'agit de dent supplémentaire (M_4), anomalie qui a été rencontrée chez divers mammifères Euthériens actuels (on figure d'ailleurs dans cette note une mandibule de *Sciurus vulgaris* qui possède bilatéralement une M_4). Les autres anomalies sont plus difficiles à interpréter, pouvant résulter soit de traumatismes affectant les germes en cours de calcification soit de variations chromosomiques. Un cas intéressant est lorsque une structure aberrante pour un genre donné devient un caractère constant chez des genres apparentés (cuspide supplémentaire linguale anormale chez *Megacricetodon* devenant fréquente chez les Myocricetodontinae puis constante (t4) chez les Dendromurinés, Cricetomyinés, Murinés).

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Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

Les gisements karstiques qui recèlent des quantités énormes de dents de micromammifères livrent exceptionnellement des spécimens aberrants sortant des limites de la variabilité des populations normales. Les quelques dents décrites dans cette note proviennent de trois fissures (L 7, M, L 3) creusées dans les calcaires bajociens de la région de La Grive-Saint-Alban (Isère). Les faunes de vertébrés recueillies dans ces fissures appartiennent á différents niveaux de l'Astaracien (MN 7 et MN 8). Le dénombrement numérique a été effectué et la fréquence de chaque forme reconnue (Mein, 1984). Comme il était prévisible, les dents anormales appartiennent aux taxons les plus communs. Ces anomalies morphologiques ont été regroupées en quatre catégories : trois qui montrent des stades successifs dans l'anormalité et une dernière regroupant des dents terminales anormalement réduites.

Observations

A. *Dents présentant un seul caractére morphologique inhabituel*

— La présence d'un tubercule impair médian á l'avant de l'antéroconide de M_1 chez *Megacricetodon gregarius* est observée dans trois cas : M_1d (1.89 × 1.13), La Grive L 7, Fig. 5 ; M_1d (1.66 × 1.07), La Grive L 7, Fig. 6 ; M_1g (1.97 × 1.07). La Grive M, Fig. 7.

Ce caractére observé est trés rare puisqu'il n'est présent que sur trois dents sur un total de plusieurs milliers. Sur deux dents, ce tubercule supplémentaire est bas et évoque le tubercule impair médian des M_1 de Muridae ; sur la plus petite des dents, ce tubercule est haut, il s'est dédoublé et forme une crête antérieure qui rejoint les antéroconides labial et lingual. L'espace creux entre cette crête et les antéroconides évoque le puiselet des M_1 de *Polonomys* (Arvicolidae).

— Le renflement en tubercule de l'antérolophide labial s'observe sur une M_1 de *Megacricetodon gregarius* : M_1g (1.74 × 1.05), La Grive M, Fig. 8. Cette dent unique offre l'originalité d'avoir un antéroconide á trois cuspides également développées. D'aprés sa position, la cuspide supplémentaire semble avoir pris naissance á partir du cingulum antéro-labial (une M_1 de *Megacricetodon lappi* de Vieux-Collonges montre également le développement d'une cuspide á partir du cingulum antéro-labial ; dans cet exemple l'antéroconide principal est simple). Ce genre de structure reste un phénoméne exceptionnel chez les Cricetodontinae. Dans plusieurs lignées de *Megacricetodon*, on assiste au cours de l'évolution á la transformation d'un antéroconide simple en antéroconide double, mais cette transformation se fait par fissuration puis bilobation de l'antéroconide á partir de son sommet sans l'intervention des cingulums. Parmi les Myocricetodontinae, un antéroconide double apparaît également dans le genre *Mellalomys* ; le nouveau tubercule dans ce cas se forme á partir du cingulum antéro-lingual (Jaeger, 1977, p. 109).

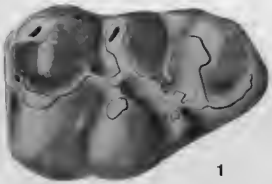
— Une cuspide linguale supplémentaire apparaît sur une M_3 d'*Heteroxerus grivensis* : M_3g (2.21 × 2.00), La Grive L 7, Fig. 14. Cette dent posséde un tubercule supplémentaire, á l'emplacement oú certains écureuils ont un petit métastyle. C'est á son niveau et non sur le bord mésial que la dent présente sa largeur maximale. Ce tubercule est aussi haut que le métaconide ; il est rejoint par l'extrémité du métalophide dont la direction est transverse. Ce tubercule semble représenter un cas de dédoublement du métaconide.

— On observe une réduction anormale d'un bord sur une M^3 d'*Heteroxerus grivensis* : M^3g (1.92 × 2.15), La Grive L 7, Fig. 13. Cette dent est caractérisée par son contour triangulaire avec un bord lingual anormalement réduit, sans trace d'hypocône. Le métalophe est réduit á un bouton en contact avec le postérolophe.

B. *Dents présentant plusieurs anomalies mais ayant conservé des portions normales permettant l'identification*

— M_1g de *Megacricetodon gregarius* (2.32 × 1.28), La Grive L 7, Fig. 10a-10b. Cette dent anormalement longue présente huit cuspides au lieu de six. Les deux cuspides supplémentaires se trouvent entre le mésolophide et l'hypolophulide ; l'une est du côté labial, l'autre du côté

Source : MNHN, Paris



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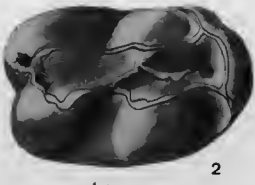

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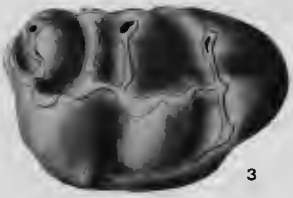

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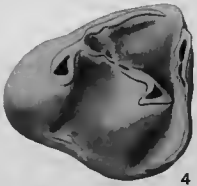

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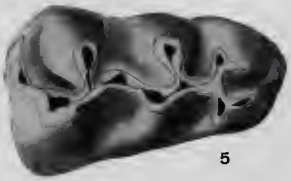

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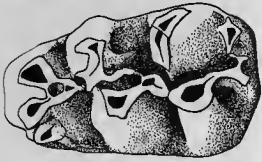

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FIG. 1. — *Democricetodon*, M¹d., vue occlusale ; La Grive L 7.
FIG. 2. — Cricetidae indet. (*Democricetodon* ?), M¹d., vue occlusale ; La Grive L 3.
FIG. 3. — *Democricetodon*, M¹d., vue occlusale ; La Grive L 3, forme normale.
FIG. 4. — *Democricetodon*, M_3 ou M_2d., vue occlusale ; La Grive L 7.
FIG. 5. — *Megacricetodon gregarius*, M_1d., vue occlusale ; La Grive L 7.
FIG. 6. — *Megacricetodon gregarius*, M_1d., vue occlusale ; La Grive L 7.
FIG. 7. — *Megacricetodon gregarius*, M_1g., vue occlusale ; La Grive M.
FIG. 8. — *Megacricetodon gregarius*, M_1g., vue occlusale ; La Grive M.

Source : MNHN, Paris

lingual. Le sinuside trés développé mésio-distale-ment est traversé par un ectomésolophide qui se renfle labialement en un fort ectostylide et se poursuit vers la base de l'hypoconide. L'anomalie de cette dent est visible également sur la racine postérieure qui, allongée mésio-distale-ment, présente un sillon sur ses deux faces latérales. Si, grâce á son antéroconide normal, l'identification spécifique est possible, cette dent est néanmoins trés aberrante ; on a l'impression qu'il y a eu un dédoublement de la partie moyenne de la dent au cours de l'ontogenése.

— M^1d de *Democricetodon* (1.77 × 1.18), La Grive L 7, Fig. 1, Cette dent de Cricetidae, en dépit de quelques ressemblances avec *Megacricetodon gregarius* (sinus oblique vers l'avant, mésolophe trés court, présence d'un cingulum antérieur), appartient trés vraisemblablement au genre *Democricetodon* á cause du contour nettement rétréci sur le bord antéro-lingual, de l'absence totale d'éperon au paracône, de la présence d'un protolophule double, et de la structure de la moitié postérieure de la dent. La moitié antérieure de la dent est trés anormale. Le protocône, pincé au lieu d'avoir la forme d'un V, n'est plus relié á l'antérocône. La branche postérieure du protolophule aboutit directement sur le protocône tandis que la branche antérieure se prolonge mésialement en antérolophule. Cet antérolophule émet un petit éperon labial, puis un fort éperon lingual qui se renfle en un tubercule lingual. L'antérolophule rejoint la portion linguale de l'antérolophe ; de ce point de jonction relativement renflé part un cingulum antéro-lingual qui atteint le point le plus mésial de la dent. L'aspect légérement bilobé de l'antérocône n'est pas comparable à ce que l'on observe chez *Megacricetodon* ; dans ce dernier genre la subdivision de l'antérocône est provoquée par l'apparition d'un sillon mésial, partant du sommet de l'antérocône, qui se poursuit plus ou moins profondément vers la base de la couronne. Ici la présence d'un cingulum antérieur crée un petit sillon vers la base de la couronne mais le sommet de l'antérolophe est rectiligne sans aucune échancrure mésiale. La forme du protocône, l'éperon lingual transformé en tubercule, le cingulum antéro-lingual sont des caractéres aberrants qui n'ont pas été retrouvés sur d'autres dents de la population.

C. *Dents á structure totalement aberrante*

— P^4g ? de Sciuridae indet. (1.82 × 2,04), La Grive L 7, Fig. 15. Cette dent maxillaire, á muraille linguale trés basse, est dépourvue de parastyle et d'antérolophe. Le protocône au milieu de la face linguale est le point de jonction de trois crétes. La crête antérieure qui rejoint le paracône possède un tubercule supplémentaire également développé situé dans la portion antéro-labiale de la dent. La deuxiéme crête semble être un métalophe renflé labialement en un métacône. La troisiéme crête est un postérolophe qui n'atteint pas le bord labial ; cette crête se renfle dans l'angle postéro-distal en un petit hypocône. On observe une muraille labiale insolite, élevée, allant du paracône au métacône et renflée en son milieu (mésostyle). Au milieu de la face mésiale et à la base de la couronne, un minuscule bourgeon d'émail peut représenter un vestige de l'antérolophe. Cette dent s'éloigne considérablement des deux Sciuridae communs du gisement. Chez *Spermophilinus* le métalophe n'atteint pas le sommet du protocône ; il n'y a pas non plus d'hypocône individualisé. Chez *Heteroxerus* il n'y a jamais de mésostyle et la muraille linguale de la dent est trés élevée.

— M^1d Cricetidae indet. (*Democricetodon* ?) (1.60 × 1.12), La Grive L 3, Fig. 2. Ce germe dentaire est constitué de quatre tubercules également développés. Les cuspides internes sont reliées par un entolophe sinueux ; la sinuosité de l'entolophe correspond á l'existence d'un sinus médian. Les deux cuspides labiales fortement coalescentes forment un ectolophe continu et rectiligne. La portion mésiale de la dent est occupée par un antérolophe plus bas qui n'est pas renflé en tubercule. Un petit cingulum lingual part du point de jonction entre l'antérolophe et l'entolophe ; de même un cingulum labial plus développé prend naissance au point de jonction entre l'antérolophe et l'ectolophe. A l'arriére de la dent un postérolophe court s'abaisse fortement. Dans la dépression centrale, entre le paracône et le protocône, une crête basse en V peut être interprétée comme un protolophule double. Le métacône se poursuit lingualement en un métalophule dont l'extrémité se subdivise en une corne mésiale et une corne distale. Le contour de la dent, la forme du protolophule et du métalophule évoquent une certaine ressem-

Source : MNHN, Paris

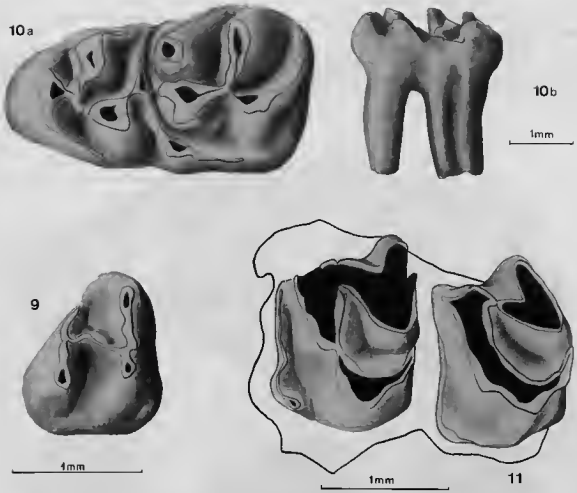

FIG. 9. — *Democricetodon*, M_3 ou M_3d., vue occlusale ; La Grive L 7.
FIG. 10. — *Megacricetodon*, M_1g ; a, vue occlusale ; b, vue labiale ; La Grive L 7.
FIG. 11. — Soricidae indet., M^1-M^2d., vue occlusale ; La Grive L 7.

blance avec le genre *Democricetodon* (comparer avec la dent représentée Fig. 3 provenant de la même localité). Ce genre est le rongeur le plus fréquent dans la fissure considérée ; il est représenté par des milliers de spécimens. Comme aucun genre de Muroidea ne présente une structure semblable à la dent décrite, on peut supposer que ce spécimen représente une dent très aberrante de *Democricetodon*.

— Fragment de maxillaire droit de Soricidae indet. M^1 (1.06 × 1.46), M^2 (1.12 × 1.51), La Grive L 7, Fig. 11. Les dents fortement usées indiquent un animal pleinement adulte. La M^2 moins aberrante que la M^1, montre un bord lingual haut avec un protocône médian ; la postprotocône-crista aboutit sur le métacône. L'hypocône très petit est rejeté sur la face distale. La dent est dépourvue d'émargination postérieure. La M^1 est plus déformée, son bord labial est réduit et oblique, le parastyle occupe une position plus distale que le paracône. Le métacône est fusionné avec le protocône en formant un métalophe. La muraille linguale a une hauteur totalement inusitée chez les Soricidae. Une telle dent isolée serait difficilement identifiable au niveau familial. En vue labiale le fragment osseux de maxillaire montre le foramen lacrymal et le canal infra-orbitaire qui ont une disposition classique de Soricidae. Le foramen lacrymal est situé au-dessus de la limite M^1-M^2 comme dans *Hemisorex robustus* (forme rare mais connue

Source : MNHN, Paris

dans le gisement) tandis que chez *Miosorex grivensis* (voir Fig. 12) ce foramen est situé au-dessus de l'arrière de M^1 ; cette dernière forme est le seul Soricidae vraiment abondant dans le gisement. Nous considérons ce spécimen comme un cas pathologique très modifié dont la forme normale correspondante ne peut être identifiée.

D. *Dernières molaires inférieures anormalement réduites*

— M_3d (ou M_4d) de *Democricetodon* (1.30 × 1.22), La Grive L 7, Fig. 4. Cette dent très réduite à l'arrière évoque le contour d'une dent de *Fahlbuschia*, mais elle n'en a ni la taille, ni la structure. L'hypoconide est pincé au lieu d'être

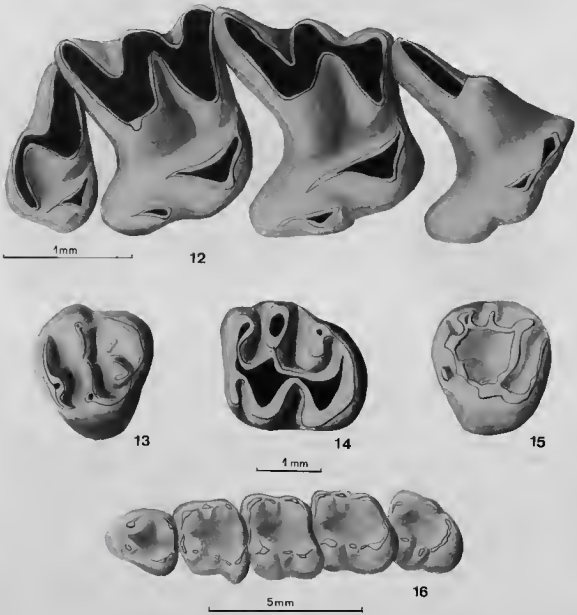

FIG. 12. — *Miosorex grivensis*, P^4-M^3d., vue occlusale ; La Grive L 7 ; forme normale.
FIG. 13. — *Heteroxerus grivensis*, M^3g., vue occlusale ; La Grive L 7.
FIG. 14. — *Heteroxerus grivensis*, M.g., vue occlusale ; La Grive L 7.
FIG. 15. — Sciuridae indet., P^4g., vue occlusale ; La Grive L 7.
FIG. 16. — *Sciurus vulgaris*, P_4-M_3g., vue occlusale ; Optevoz F-38, actuel.

Source : MNHN, Paris

en croissant ; il n'y a ni postérolophide, ni postérosinuside. L'ectolophide n'aboutit pas directement sur l'hypoconide mais sur l'hypolophulide. On observe un minuscule mésolophide libre. L'antérolophide labial est normalement développé mais l'antérolophide lingual a entièrement disparu. Le métalophulide directement sur le bord mésial de la dent est isolé du protoconide. La structure de la partie médiane de la dent permet de l'attribuer au genre *Democricetodon*. Chez *Fahlbuschia* en effet l'ectolophide est plus oblique, l'hypolophulide et le mésolophide sont largement fusionnés et atteignent le bord lingual de la dent.

— M_3d (ou M_4d) de *Democricetodon*? (1.10 × 1.25), La Grive L 7, Fig. 9. Ce spécimen encore plus aberrant que le précédent allie à une régression de la partie postérieure, une forte compression de la partie antérieure. L'antérolophide labial, vestigial, est cantonné à la base de la couronne. Le métalophulide aboutit directement sur le protoconide ; une telle disposition ne s'observe habituellement que chez les Eomyidae. La dent est devenue plus développée dans le sens vestibulo-lingual que dans le sens mésio-distal. La moitié postérieure de la dent offre la même structure aberrante que celle observée dans le spécimen précédent et c'est cette comparaison qui permet d'envisager l'appartenance à un *Democricetodon*.

Discussion

Les anomalies limitées à un caractère morphologique sont plus fréquentes que les autres ; elles portent essentiellement sur les portions de dents ayant déjà une forte variabilité naturelle. Ces anomalies sont probablement d'origine chromosomique ; elles peuvent, le cas échéant, illustrer des parentés phylétiques entre différents groupes. Parmi les dents fossiles examinées, les anomalies de l'antéroconide des *Megacricetodon* entrent dans cette catégorie. Les anomalies profondes, connues par un seul exemplaire, correspondent probablement à des accidents pathologiques survenus au cours de l'ontogenèse. Les dernières molaires inférieures anormalement réduites correspondent probablement à des molaires surnuméraires (M_4). Ce phénomène est moins connu chez les rongeurs que dans d'autres ordres de mammifères ; il est mentionné chez un Zapodidae actuel (Krutzsch, 1953). Nous avons par hasard récolté, tué par une voiture, un spécimen de *Sciurus vulgaris* qui possède bilatéralement des M_4. La série dentaire gauche de cet animal (Fig. 16) a pour mensurations : L. P_4-M_4 : 11,25 ; L. P_4-M_3 : 9,23 ; P_4 : L. 2,23-l. 2,25 ; M_1 : L. 2,30-l. 2,66 ; M_2 : L. 2,86-l. 2,65 ; M_3 : L. 2,86-l. 2,65 ; M_4 : L. 2,55-l. 2,34.

La M_4 a des cuspides dont le nombre et la position sont comparables à ce que l'on observe sur la M_3. La dent est plus petite avec un bord mésial plus oblique. Le bord labial est bien plus court que le bord lingual. La mandibule, en vue labiale, montre que le départ de la branche montante occulte la moitié postérieure de la M_3. Cette position relative est identique à celle des écureuils normaux ; la présence d'une dent surnuméraire n'a affecté ni la position ni la morphologie des autres dents. Les rares cas de molaires anormales signalés en paléontologie se rapportent presque tous à des M_4 : *Pelycodus* (Wilson, 1955) ; *Anancus* (Viret, 1962) ; *Sivapithecus* (Tattersall & Simons, 1969). Enfin les molaires intermédiaires : M2 de Cricetidae, M1-2 de Sciuridae sont les plus stables ; aucune anomalie n'a été décelée dans le matériel examiné.

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Dental Morphology and Odontometrics of Early Agriculturalists from Neolithic Mehrgarh, Pakistan

J. R. LUKACS

ABSTRACT

Human burials were discovered by the French Archaeological Mission to Pakistan during the excavation of Neolithic levels at Mehrgarh in Baluchistan Province. Human skeletal remains from this important pre-Harappan site provide our first glimpse of the dental morphology and tooth size of early agriculturalists on the western fringe of the Indus Valley. Morphological variations of both permanent and deciduous teeth were observed and graded according to standardized trait classifications. Mesiodistal and buccolingual crown diameters of permanent and deciduous teeth were recorded and statistically analyzed.

Permanent and deciduous teeth at Mehrgarh are complex in morphology and large in size when compared with other human skeletal series from southern Asia. The Neolithic inhabitants of Mehrgarh exhibit a dental pattern that is similar and possibly ancestral to Chalcolithic populations of west-central India, but which is clearly distinct from living inhabitants of north India and Epipaleolithic skeletal series from the Near East. Tooth size variation between Neolithic populations of the Near East, Pakistan, and Southeast Asia is small and may reflect similar subsistence techniques and varying ecological settings.

RÉSUMÉ

Des sépultures humaines ont été découvertes par la Mission Archéologique Française au Pakistan au cours de fouilles dans les niveaux néolithiques de Mehrgarh, dans la province du Baluchistan. Les restes squelettiques humains provenant de cet important site pré-Harrapéen nous fournissent une première image de la morphologie dentaire et de la taille des dents des premiers agriculteurs installés sur la rive occidentale de la vallée de l'Indus. Des variations morphologiques des dents permanentes et lactéales ont été observées et ordonnées selon les classifications standardisées des caractères. Les diamètres mésio-distal et bucco-lingual de la couronne des dents permanentes et lactéales ont été mesurés et analysés statistiquement.

Les dents permanentes et lactéales de Mehrgarh sont de morphologie complexe et de grande taille par comparaison avec d'autres séries squelettiques humaines d'Asie méridionale. Les habitants néolithiques de Mehrgarh présentaient un dessin dentaire semblable, et peut-être ancestral, à celui des populations chalcolithiques de l'Inde occidentale et centrale, mais nettement distinct de celui des habitants actuels de l'Inde septentrionale et des séries squelettiques épipaléolithiques du Proche-Orient. La variation de taille des dents entre les populations néolithiques du Proche-Orient, du Pakistan et de l'Asie du Sud-Est est faible et peut refléter des techniques voisines de subsistance et un environnement écologique variable.

In: Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 285-303.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

Dental morphology and tooth-size variations for Neolithic populations of southern Asia are poorly documented. This situation is paradoxical given the importance of this geographic region during the course of human biological and cultural evolution, and the potential contribution dental anthropology can make toward the solution of crucial anthropological problems.

The pattern of dental variation for people of the Indus Valley Civilization is poorly known despite the recovery of abundant human skeletons from Harappa (Gupta *et al.*, 1962) and Mohenjo-Daro (Sewell & Guha, 1931; Guha & Basu; 1938). Until recently, skeletal and dental evidence from sites antecedent to the Indus Civilization was virtually non-existent. Since the mid-1970s the French Archaeological Mission to Pakistan has been excavating Neolithic human skeletons with well preserved dentition at Mehrgarh, in the north Kachi Plain of Baluchistan Province. This material provides, for the first time in South Asia, sufficient evidence for the study of dental anthropology among early agriculturalists of this region. The objective of this paper is to provide a thorough description and comparative analysis of dental morphology and tooth-size of the pre-Harappan Neolithic skeletal sample from Mehrgarh.

A research landmark in the dental anthropology literature on prehistoric Asian skeletal remains was Dahlberg's (1960) description of the dentition of early agriculturalists from Neolithic Jarmo (Iraq) in 1960. Subsequent investigations of the dental morphology and pathology of Natufian skeletal series were conducted by Smith (1970; Smith *et al.*, 1984). The dental anthropology of a small sample of Neolithic human skeletons from Abou Gosh was reported on by Arensburg *et al.* (1978), and a study of tooth-size and crown morphology of 49 specimens from the Neolithic site of Ganj Dareh Tepe in Western Iran is currently in progress (Lambert, 1980; Meiklejohn, pers. comm.; Smith, 1974). The rate of dental research in southwest Asia has been slow but steady and prehistoric patterns of dental variation are becoming clearer.

In contrast, the dearth of dental data for Neolithic inhabitants of the Indian subcontinent (South Asia) and southeast Asia precludes effective inter- and intra-regional comparisons for southern Asia as a whole (Lukacs, 1984). Human remains from late Neolithic sites of peninsular India are common (Brahmagiri, Wheeler, 1947; Maski, Thapar, 1957; Piklihal, Allchin, 1961; Tekkalakota, Nagaraja Rao, 1965), but their young age (3000-2000 B.C.), small sample size and undescribed dentition precludes direct comparison with samples from Neolithic horizons in the northwest (Possehl & Rissman, in press). Descriptive and comparative reports on these skeletal remains were published but are woefully incomplete (Brahmagiri & Maski, Sarkar, 1960, 1972; Piklihal, Ayer, 1961; Malhotra, 1967; Tekkalakota, Malhotra, 1965).

Dental morphology and odontometrics were reported for Neolithic Burzahom in Kashmir (Basu & Pal, 1980), and for Mesolithic Sarai Nahar Rai and Mahadaha in the Gangetic Basin (Kennedy, 1984; Kennedy *et al.*, 1986). These latter sites are perhaps more suitable as a comparative framework against which the Neolithic Mehrgarh dental variation can be analyzed, but thorough dental documentation is unavailable, and sample sizes are small. Southeast Asian Neolithic burials are few, though Brace & Vitzthum (1984) recently reported on tooth-size at Mesolithic, Neolithic and modern levels at Niah, Cave, Sarawak and Pietrusewsky (n.d.) has described the dental remains from Ban Chiang.

Previous reports on the human remains from Mehrgarh include descriptions of funerary practices (Samzun & Sellier, in press), demography (Samzun & Sellier, 1983; Sellier, in press), dental pathology and tooth-size (Lukacs, 1985b; Lukacs, 1983a; Lukacs *et al.*, 1985).

The dental data reported here for Neolithic occupants of the northwest borderlands of the Indian subcontinent fills a crucial lacuna in our record of prehistoric dental variation in southern Asia, and should contribute to the solution of anthropologically important questions such as:

1. Is there genetic continuity between Neolithic and early Chalcolithic people at Mehrgarh?
2. Could the people of Mehrgarh be ancestral to the builders of the Indus Valley Civilization?
3. What is the genetic relationship between the Neolithic people of Mehrgarh and contemporaneous people of Iran-Afghan highlands?

Source : MNHN, Paris

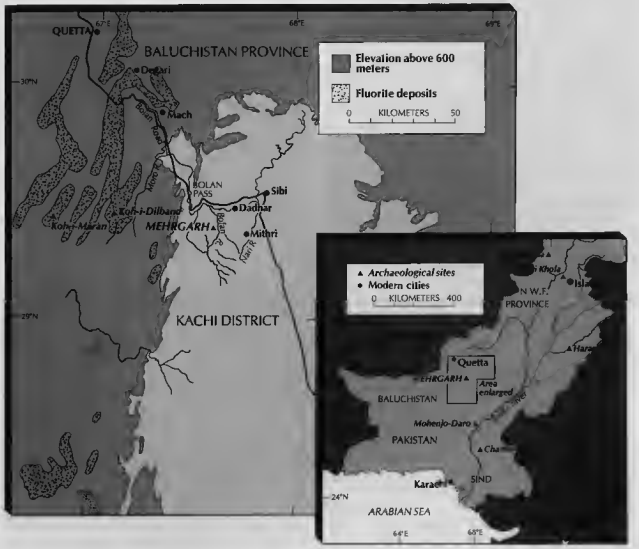
4. Which prehistoric people of the Indian subcontinent are most closely related to the Neolithic occupants of Mehrgarh?
5. To which living people of the Indian subcontinent are the people of Mehrgarh most closely related?

The study of dental morphology at Mehrgarh was begun with these questions in mind.

Material and Method

The site of Mehrgarh, encompassing about 500 acres, is located at the foot of the Bolan Pass, on the west bank of the Bolan River, and has been under excavation by the French Archaeological Mission for 11 seasons (Fig. 1). Three main areas of the site have been intensively excavated (from north to south): MR3—Early Neolithic; Period I; MR2—Chalcolithic, Period III; and MR1-late Chalcolithic, Periods V through VII (Jarrige, 1984; Jarrige & Lechevallier, 1979; Jarrige & Meadow, 1980).

The antiquity of early Neolithic levels at Mehrgarh is based on radiocarbon dates and cross-dating, which place the beginning of Period I prior to 6000 B.C. (Jarrige, 1984; Jarrige & Lechevallier, 1980). Geomorphologically MR3 is complex, consisting of two overlapping buried mounds (11 m in depth); the apices were subsequently eroded by sheetwash to the level of the surrounding plain. The transition from aceramic,



Source : MNHN, Paris

predominantly huntergatherer folk to pottery-using agriculturalists with domesticated cattle, sheep, and goat is well documented in Periods I and II (Lechevallier & Quivron, 1981; Meadow, 1981, 1983, 1984). Plant remains from MR3 were identified by Costantini (1984) who found two types of barley and three of wheat.

Human burials, containing bones varying in the quality of preservation, are moderately abundant in all excavated areas at Mehrgarh. Grave goods are often in the burials and include blade tools, ground stone axes, baskets lined with bitumen, ornaments of turquoise and lapis lazuli, and, in a few cases, the apparently sacrificial remains of several young goats (Lechevallier *et al.*, 1982; Lechevallier & Quivron, 1981). Neolithic burials are normally interred on the left side with knees and arms tightly flexed. The body is oriented toward the south, often facing a wall of handmade, unbaked mud brick.

The human skeletons on which this study is based are from the "upper graveyard" in the MR3 excavation area (n = 41 individuals) and from roughly contemporaneous burials (n = 22) adjacent to it. In order to maximize the dental sample an additional 27 individuals from MR3 were included in the analysis (MR3F, MR3T, MR3S). These specimens are derived from horizons adjacent to and below the "upper graveyard", and consequently are not *strictly* contemporary with the graveyard sample.

Morphological variations of permanent dental crowns were assessed by reference to standards depicted in plaster models and/or published photographs. The morphological traits included in this description of the Mehrgarh dentition are listed below along with the primary sources describing or depicting categories of trait variation:

Maxillary Incisor Teeth

1. Shovel-shape (Hrdlička, 1920; Dahlberg, 1963; Scott, 1980).
2. Double-shovel (Turner, 1967).
3. *Tuberculum dentale* (Turner, 1967).
4. Marginal interruption grooves (Turner, 1967).
5. Lingual tubercles (Turner & Scott, 1977).

Maxillary Molar Teeth

6. Hypocone development (Dahlberg, 1951).
7. Carabelli's trait (Dahlberg, 1963; Scott, 1980).
8. Metaconule variation (Harris & Bailit, 1980).
9. Protoconule variation (Turner, 1967).
10. Parastyle (Turner, 1967).

Mandibular Molar Teeth

11. Groove pattern (Hellman, 1928; Jorgensen, 1955).
12. Cusp number (Hellman, 1928).
13. Entoconulid variation, C-6 (Turner, 1970).
14. Metaconulid variation, C-7 (Turner, 1970).
15. Protostylid (Scott & Dahlberg, 1982).
16. Deflecting wrinkle (Scott & Dahlberg, 1982).
17. Three rooted first molar (Turner, 1971).

The scoring of deciduous dental traits follows the standards outlined by Hanihara (1963, 1965; Hanihara & Minamidate, 1965) in the analysis of deciduous teeth of Japanese-American hybrids. Included in this study are many of the traits recognized by Hanihara (1966, 1968) as comprising the Mongoloid Dental Complex of the deciduous dentition. Deciduous dental traits observed include: 1) shovel-shape of central and lateral incisor teeth, 2) *tuberculum dentale* of dc, 3) cusp number of dm^1 and dm^2, 4) Carabelli's trait of dm^2, 5) labial (facial) deflection of di^1 root apex, 6) cusp number of dm_1 and dm_2, and accessory cusps of dm_2, including, 7) the entoconulid (cusp 6), 8) the metaconulid (cusp 7), and 9) the protostylid. Three variables were excluded from analysis due to inconsistent grading, rapid obliteration of the trait with attrition, or the frequent occurrence of intermediate categories. These traits include the distal trigonid crest, deflecting wrinkle and groove pattern of dm_2.

In tabulating dental trait frequencies, the individual count method of Scott (1977, 1980) was used. This technique counts the fullest expression of a given trait on either the right or left side of the jaw; if one side is missing the degree of expression on the side present is scored. Each individual is counted only once for each variable. This technique maximizes sample size in fragmentary skeletal samples derived from archaeological contexts and is well suited for the Mehrgarh dental sample.

Dental trait frequencies were calculated for each degree of expression of a trait. Prior to comparative statistical analysis (chi-square) of trait frequencies, an investigation of the correspondence of trait categories (used in this study and by others) was undertaken to ensure equivalence of trait classes being compared.

Two measures of crown size were made for each tooth: maximum mesiodistal diameter (MD) and maximum buccolingual diameter (BL), fol-

Source : MNHN, Paris

lowing the method described by Moorrees (1957). All measurements were made by Lukacs with a Helios needle-point dial caliper calibrated to 0.05 mm. Replicate measurements made more than two days apart on permanent Mehrgarh teeth yielded a mean measurement error of 0.10 mm. (SD = 0.126, n = 70) for MD diameter and 0.07 mm. (SD = 0.084, n = 74) for BL diameter. These values fall well within the acceptable range of measurement error reported by Wolpoff (1971). Linear crown dimensions were employed in calculating the dental index Crown Area (MD times BL), which serves as a measure of the cross-sectional area of the crown (Wolpoff, 1971).

Results

A. *Dental Morphology*

Dental trait frequencies for permanent teeth are presented in Tables 1-3. Morphological variation in maxillary anterior teeth is presented in Table 1. Shovel-shaped incisor and canine teeth are common at Mehrgarh. The frequency of shovelling decreases distally, from central incisor to lateral incisor to canine, and intermediate grades of expression are more prevalent than full expression of the trait. Cingular tubercles are nearly three times more frequent in maxillary canine teeth than in lateral incisors. While rare in lateral incisors, the *tuberculum dentale* (= median lingual ridge) is present in fifty-eight percent of central incisor teeth. Marginal interruptions are absent from central incisors, but fifty-one percent of maxillary lateral incisors display the trait. Interruptions occur with equal frequency on the mesial and distal margins of the tooth crown.

Table 2 provides frequency data for morphological variations of maxillary molar teeth. Carabelli's trait is present in twenty-six percent of first molar teeth, but weak expressions (pit and groove forms) of the trait are twice as common as full-cusp expressions. Carabelli's trait is conspicuous by its absence from seventy-four percent of first molar teeth. Hypocone variation follows a typical pattern of size gradation from M1 (83.3 %, grade 4) to M2 (73.1 %, grade 4—) to M3 (79.4 %, grade 3+), with M1 the least variable and M3 the most variable tooth. Complete absence of the hypocone was not detected in first or second molars and was observed in only 5.9 % of third molar teeth. The metaconule is more frequent than the protoconule in M1 and this difference in frequency becomes greater in M2 and M3. The parastyle is present in low frequency in M2 and M3, but absent in M1.

Morphological variations in mandibular molar teeth are presented in Table 3. Due to occlusal attrition, groove pattern was discernable less often than cusp number, a factor that explains the difference in sample size for these variables. The most prevalent groove configuration varied by tooth, with 92 % Y in M1, 48.6 % + in M2 and 63 % X in M3. Variation in lower molar cusp number was greatest in M3 and least in M2. The most frequent cusp number sequence was M1 — 5; M2 — 4, M3 — 5, with 74.4 % of M1s exhibiting five cusps, 93.9 % of M2s four-cusped and 63 % of M3s five-cusped. Accessory lower molar cusps occur with moderate to low frequency. The entoconulid (C-6) was present in 8.1 % and the metaconulid (C-7) was found in 10 % of first molars.

Strong expressions of the protostylid were detected in the Mehrgarh sample but in low frequency (5 %) and three-rooted lower first molar teeth also occur rarely (5.6 %). Problems of recognizing weak expressions of the former under field lighting conditions and diagnosis of the latter, macroscopically and without the aid of radiographic plates results in small sample size for these traits. The frequencies reported for these traits should, therefore, be considered as tentative estimates rather than firm data points.

Variation in deciduous dental morphology is presented in Table 4. Though sample sizes are small for all traits considered, some idea of trait expression can be derived from these data. Shovel-shape is more common, especially weak expressions, in central than in lateral deciduous teeth. *Tuberculum dentale* is very frequent (83.3 %) in maxillary deciduous canine teeth, but is absent from maxillary incisors. The circular enamel defect (hypoplasia), a trait of uncertain etiology, is more common in lower deciduous canines (42 %, n = 19) than in maxillary canines (17 %, n = 24), a finding in agreement with Skinner (1986). The overall prevalence of this anomalous localized form of hypoplasia is 27.9 % (n = 43) in deciduous canines at Mehrgarh (MR3).

Source : MNHN, Paris

Weak expressions of Carabelli's trait (grades 1-3; pit and groove forms) are common (74.7 %, n = 11) in dm^2, and this tooth typically exhibits a full-sized hypocone (grade 4). Lower deciduous molar cusp number is more variable in dm_1 than in dm_2, where 72.7 % (n= 11) are five-cusped. Accessory cusps of dm_2 exhibit high frequencies, with the protostylid (37.5 %, n = 8) and entoconulid (27.3 %, n = 11) occurring more often than the metaconulid (9.1 %, n = 11).

Results of this morphological analysis of the Neolithic teeth from Mehrgarh can be succinctly summarized for permanent and deciduous teeth separately.

PERMANENT TEETH:

- — maxillary anterior teeth are highly sculpted, i.e., exhibit high frequencies of shovelling, lingual tubercles, lingual ridges and pits and marginal grooves;
- — maxillary molar teeth have a low incidence of Carabelli's trait and the hypocone exhibits little reduction and is rarely absent;
- — mandibular molar teeth are conservative morphologically and accessory cusps occur in moderate to low frequencies.

DECIDUOUS TEETH:

- — maxillary anterior teeth are frequently but weakly shovelled, and canines often display *tuberculum dentale*;
- — maxillary molar teeth exhibit fully developed hypocones and Carabelli's trait, though common, is weakly expressed.
- — mandibular molar teeth are morphologically complex and accessory cusps are common.

In comparing trait frequencies in permanent and deciduous dentitions at Mehrgarh, several noteworthy observations can be made. Particular dental traits display higher frequencies in the deciduous teeth than in their permanent successors (Carabelli's trait, *tuberculum dentale* of the canine, accessory cusps of the lower molar, including C-6, protostylid); while others are less common in deciduous teeth (shovel-shape, C-7) than in permanent teeth.

B. *Odontometrics*

Mean mesiodistal (MD) and buccolingual (BL) crown diameters for permanent and deciduous dental samples from Neolithic Mehrgarh are presented in Tables 5 and 6, together with relevant descriptive statistics (in mm., left side only).

The analysis of permanent tooth crown dimensions initially divided the dental sample into three groups for comparative analysis: Period IA, Period IB, Period I-level uncertain. While crown dimensions of teeth from IA were consistantly larger in MD and BL diameters than teeth from IB, these differences rarely attained statistical significance at the .05 level. The tendency toward reduced dental crown dimensions within the Mehrgarh Neolithic from earlier Period IA to later Period IB is suggested by the fact that : 1) all five significant differences are toward smaller teeth in IB, and 2) 78 % of MD and BL comparisons on the left and 84 % of the comparisons on the right show smaller crown diameters for IB teeth compared to the IA sample. Table 7 presents comparative data by Period for the analysis of diachronic change in dental dimensions at Mehrgarh.

The deciduous dental sample is too small to permit an analysis of diachronic change within Neolithic levels at Mehrgarh. The standard deviation for BL diameters of deciduous teeth is uniformly less (by .05 to .23) than the standard deviation for MD diameters. This may be due to the combined effects of greater genetic control over MD tooth size (selected for by jaw space constraints) and the greater accuracy and repeatability of measuring BL diameters.

The overall similarity in dimension of permanent teeth from Periods IA and IB justified using the entire Neolithic sample in computing cross-sectional tooth crown areas (MD × BL). This product was computed for each tooth individually then descriptive statistics were generated for each new variable. Table 8 presents mean tooth crown area figures and appropriate statistics for the left side of the dental arcade. When tooth crown areas are summed across all teeth the resulting total crown area is 1257.82 mm^2. The maxillary teeth as a unit make a larger (658.71 mm^2) contribution to total crown area (52.37 %) than the mandibular teeth (599.11 mm^2; 47.63 %). These figures are remarkably similar to

Source : MNHN, Paris

preliminary results obtained on smaller samples in 1985 (Lukacs *et al.*, 1985).

Mean cross-sectional crown areas for deciduous teeth are presented in Table 6, which reveals a total deciduous crown area of 533.59 mm^2. As in the permanent teeth, the maxillary dentition contributes more to total crown area (286.80 mm^2; 53.75 %) than does the mandibular dentition (246.79 mm^2; 46.25 %).

This descriptive analysis of the deciduous teeth from Neolithic Mehrgarh serves as a tentative and preliminary account. The possibility of bias in these small samples of deciduous teeth demands that the results be regarded with caution.

Discussion

Comparative assessment of dental morphology at Neolithic Mehrgarh is hampered by several factors: 1) paucity of skeletal remains from appropriate temporal and geographical contexts, 2) varying trait classification standards employed by different researchers, and 3) small sample size of most prehistoric skeletal series (Lukacs, 1984).

Comparative dental trait frequencies for twelve often studied variables are presented in Table 9 for prehistoric south Asian skeletal series. All samples were studied by Lukacs (1983b; Lukacs *et al.*, 1983) personally thereby reducing a prime source of uncertainty in comparative analyses — inter-observed variance.

The grades of expression employed in calculating the frequency of each trait are outlined below (many follow Scott & Dahlberg, 1982):

1. Shovel-shape (I^1): Only the full-shovel expression (Hrdlička, 1920), equivalent to the pronounced grades of Scott & Dahlberg (1982), was counted in calculating the frequency of this trait.
2. Median Lingual Ridge (I^1): Also known as *Tuberculum dentale*, any development of ridging on the lingual surface between the mesial marginal and distal marginal ridges was scored as present.
3. Marginal Interruption (I^1, I^2): Any groove extending from the lingual fossa across the mesial, distal or medial (cingular) marginal ridge. All expressions of the trait are graded as present in calculating trait frequency.
4. Cingulum Variation (I^1): One or more lingual grooves on the cingulum of maxillary central incisors. Any expression graded as present and used in calculating trait frequency.
5. Hypocone Size (M^1): The frequency reported for this trait includes only the fully developed expression (grade 4, Dahlberg, 1951). Grades 3, 3+, and 4— are considered as underdeveloped expressions of the trait and were not counted in computing this trait's frequency.
6. Carabelli's trait (M^1): All morphological variants occurring on the mesio-buccal aspect of the mesio-buccal cusp (groove, pit, pit and groove, or cusp of varying size) were counted in computing the frequency of this trait.
7. Metaconule, C-5 (M^1): Located between the metacone and the hypocone of maxillary molar teeth, any expression of this supernumerary cusp was counted in calculating its trait frequency.
8. Cusp Number (M_2): The presence of a hypoconulid (C-5) of any size, resulting in a five-cusped lower second molar, was counted in calculating the frequency of this trait.
9. Deflecting wrinkle (M_1): A conspicuous bend or deflection of the metaconid ridge was graded as present. A straight or slightly diverted ridge was graded as absent in computing the frequency of this trait.
10. Entoconulid, C-6 (M_1): Also termed the *tuberculum sextum* (Hellman, 1928), C-6 is located between C-4 and C-5 on the lower molar crown and varies continuously in size when present. All size variants were counted in computing the frequency of this trait.
11. Metaconulid, C-7 (M_1): This supernumerary cusp, also called the *tuberculum intermedium* (Hellman, 1928), is located on the lingual margin of the lower molar crown between C-2 and C-4. All cusp variants of this trait were counted in calculating the frequency of this trait.

Source : MNHN, Paris

12. Protostylid (M_1): Expressions of this trait graded as present include a groove, fissure or cusp of varying size on the mesiobuccal cusp of lower molar teeth (Dahlberg, 1950). Variations of the buccal pit were not included as part of this trait complex.

The chi-square test of intergroup differences was applied to the twelve traits in Table 9. In none of the comparisons was Inamgaon or Timargarha significantly different from the Neolithic Mehrgarh sample at the level of 0.05. The Sarai Khola series exhibited significant differences from Mehrgarh for three variables: median lingual ridge (1^1), marginal interruption (1^2) and deflecting wrinkle (M_1). These results suggest that the Neolithic occupants of Mehrgarh are more similar in dental morphology to the people of Inamgaon and Timargarha than they are to the sample from Sarai Khola. The consequences of small sample size on statistical analysis of this kind renders these conclusions tentative and subject to confirmation based on more complete evidence.

Further scrutiny of dental trait frequencies in Table 9 shows that the Mehrgarh teeth are different (though not significantly) from other prehistoric south Asian skeletal samples in having:

— a higher frequency of morphological variations present in maxillary incisor teeth, (not shown in Table 9 is the higher frequency of shovelling and cingular tubercles in maxillary canines which also distinguishes the Mehrgarh sample from other south Asian prehistoric groups);
— a lower incidence of Carabelli's trait, and
— a higher frequency of traits that contribute to molar crown complexity (accessory cusps, large hypocone (-id), and deflecting wrinkle).

From this analysis the Neolithic occupants of Mehrgarh display a morphologically complex dentition which could have been ancestral to the dental patterns at Inamgaon and Timargarha, but which seems less closely related to the more simplified dental pattern at Sarai Khola. Dental morphology at Neolithic Mehrgarh is much more complex than trait frequencies for modern Hindus of north India (Zubov, 1980) and Indian immigrants in South Africa (Scott, pers. comm.). Recent north Indian caste groups appear to have less incisor shovelling and cingular tubercles, higher incidence of Carabelli's trait and fewer accessory cusps of lower molars. Their dental pattern compares favorably with the simplified dental morphology reported for Sarai Khola, and contrasts strongly with the complexly structured dentition from Mehrgarh.

Except for the work of Kaul & Prakash (1981) on Jats, and Lukacs & Walimbe (1984) on prehistoric Inamgaon, few anthropologically valid studies of deciduous crown morphology are available for the Indian subcontinent. In comparison with these samples (see Table 10) the Neolithic deciduous teeth from Mehrgarh exhibit similarities to Inamgaon and modern Jats in maxillary central incisor shovelling (grade 2-3), Carabelli's trait (grade 4-6), and cusp number (2 cusped dm^1). The Mehrgarh sample is distinguished from Jats and/or occupants of Inamgaon by the prevalence of *tuberculum dentale* in maxillary canines, the higher frequency of grade 4 hypocone (dm^2) and accessory cusps (C-6, C-7 and protostylid). The chi-square test of inter-group differences between Mehrgarh and Inamgaon reveals only one significant difference (protostylid, = 0.01) in nine comparisons while the Mehrgarh-Jat contrast indicated differences in five traits (*tuberculum dentale*, dc; cusp number, dm^2 and dm_2; accessory cusps C-6, C-7 in dm_2) of seven comparisons. These results suggest a closer relationship between the Mehrgarh sample and the people of Inamgaon than between Mehrgarh and the modern Jats of north India.

Inter-observer variance and disparate sample sizes undoubtedly have some influence on results of the Mehrgarh-Jat comparison, but this degree of difference was not unexpected. Permanent dental morphology also points to significant divergence of modern north Indians from Neolithic occupants of Mehrgarh.

Comparative evaluation of tooth size at Neolithic Mehrgarh is facilitated by using the summed cross-sectional crown area. This figure is favored by some investigators because it represents the unit on which natural selection operates, and because direct comparisons can easily be made (Brace, 1980). Table 11 presents summed crown areas (mm^2) for permanent teeth of selected prehistoric skeletal series from southern Asia. The figure for Mehrgarh (1257 mm^2) falls squarely within the range of values reported by others for Neolithic dental samples from southwest Asia.

Source : MNHN, Paris

The mean summed crown area for four Neolithic groups (Jericho, Natufian, Jarmo and Abou Gosh) coincides with the figure of 1257 mm^2 reported here for Mehrgarh.

It is noteworthy that in dental morphology the Natufians are distinct from Neolithic inhabitants of Mehrgarh, but that the close correspondence of tooth size figures may represent evolutionary convergence (Lukacs, in press). From different gene pools both Natufian and Mehrgarh samples arrived at a similar optimal tooth size. Similar selective pressures related to shared patterns of subsistence, diet and food preparation methods are the most likely causes for this convergence in tooth crown area.

Mean crown areas for deciduous teeth of prehistoric and living south Asians are provided in Table 12 for comparison with the Mehrgarh data. The prehistoric samples were studied by Lukacs (Lukacs *et al.*, 1983), the living Gujaratis by Makhija (1981). The Mehrgarh deciduous teeth are uniformly larger in crown area than all other south Asian deciduous dental samples. The percentage by which tooth crown area of living and prehistoric samples are smaller than Mehrgarh teeth (in maxillary, mandibular and total crown area) is given in brackets after the summary tooth crown size figure. The size difference is least in the mandibular crown area at Inamgaon (6.51 %) and greatest in the mandibular teeth at Timargarha (12.26 %). Kaul & Prakash (1984) recently reported on crown dimensions of north Indian Jats in Harayana State. Teeth for which crown area can be computed (maxillary and mandibular deciduous molar teeth) are smaller than the Gujarat sample and much smaller than deciduous molars from Mehrgarh.

The direction of deciduous tooth-size variation reported here for prehistoric south Asians coincides with predictions based on Brace's hypothesis that populations with a longer dependence on agriculture and more sophisticated food preparation methods will have smaller teeth (Brace, 1962, 1978, 1984). This prediction was tested extensively by Brace with permanent tooth-size data, but has not been widely tested with deciduous tooth-size data.

Conclusion

This study of dental morphology and tooth size at Neolithic Mehrgarh provides our first impression of the dental pattern of early (pre-Harappan) agriculturalists in South Asia. The permanent and deciduous teeth at Mehrgarh are morphologically complex and crown dimensions are large (megadont).

Anterior permanent maxillary teeth (I, C) exhibit a distinctive trait complex including shovelling, *tuberculum dentale*, marginal interruption grooves and median lingual ridges. Molar tooth morphology combines a low incidence of Carabelli's trait with moderate to high frequencies of accessory cusps.

Comparative samples from the subcontinent are rare but dental morphology of permanent teeth suggests a closer biological relationship between Mehrgarh and skeletal series from Inamgaon (India) and Timargarha (Pakistan), than between Mehrgarh and Sarai Khola (Pakistan).

The morphological complexity of deciduous teeth is discernable in the high frequency of *tuberculum dentale* (dc), retention of a large hypocone (dm^2), and prevalence of accessory cusps (dm_2). The clear contrast in deciduous dental trait frequencies between Mehrgarh and modern Jats of north India indicate little if any biological relationship between them. The similarities in deciduous tooth morphology between Inamgaon and Mehrgarh strongly suggests a biological relationship between them. People with a dental pattern like that found at Mehrgarh could well have been ancestral to later Chalcolithic inhabitants of western and central India.

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Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Morphological variations of maxillary anterior teeth.

SHOVEL SHAPE

	I^1		I^2		C	
grade	n	(%)	n	(%)	n	(%)
0	3	(10.7)	6	(16.2)	6	(25.0)
1	7	(25.0)	14	(37.8)	11	(45.8)
2	15	(53.6)	14	(37.8)	7	(29.2)
3	3	(10.7)	3	(8.2)	0	(0.0)
Total	28	(100.0)	37	(100.0)	24	(100.0)

CINGULAR TUBERCLE

	I^2		C	
grade	n	(%)	n	(%)
0	27	(84.4)	15	(55.6)
1	5	(15.6)	12	(44.4)
Total	32	(100.0)	27	(100.0)

MEDIAN LINGUAL RIDGE

	I^1		I^2	
grade	n	(%)	n	(%)
0	11	(42.3)	27	(93.2)
1	4	(15.4)	1	(3.4)
2 (TD)	11	(42.3)	1	(3.4)
Total	26	(100.0)	29	(100.0)

MARGINAL INTERRUPTION

	I^1		I^2	
grade	n	(%)	n	(%)
0	27	(100.0)	15	(48.4)
1 (mésial)	0	(0.0)	7	(22.6)
2 (distal)	0	(0.0)	7	(22.6)
3 (median)	0	(0.0)	2	(6.4)
Total	27	(100.0)	31	(100.0)

TABLE 2. Morphological variations of maxillary molar teeth.

CARABELLI'S TRAIT (M^1)

grade	n	(%)
0	20	(74.0)
groove (1-3)	4	(14.8)
y (4)	1	(3.8)
cusp (5-7)	2	(7.4)
Total	27	(100.0)

HYPOCONE VARIATION

	M^1		M^2		M^3	
grade	n	(%)	n	(%)	n	(%)
4	35	(83.3)	2	(4.9)	1	(2.9)
4—	7	(16.7)	30	(73.1)	4	(11.8)
3+	0	(0.0)	9	(22.0)	27	(79.4)
3	0	(0.0)	0	(0.0)	2	(5.9)
Total	42	(100.0)	41	(100.0)	34	(100.0)

	M^1		M^2		M^3	
	n	(%)	n	(%)	n	(%)
Metaconule						
grade 0	21	(75.0)	15	(60.0)	11	(57.9)
1	7	(25.0)	10	(40.0)	8	(42.1)
Total	28	(100.0)	25	(100.0)	19	(100.0)
Protoconule						
grade 0	17	(81.0)	22	(100.0)	14	(82.4)
1	4	(19.0)	0	(0.0)	3	(17.6)
Total	21	(100.0)	22	(100.0)	17	(100.0)
Parastyle						
grade 0	38	(100.0)	34	(97.1)	30	(96.8)
1	0	(0.0)	1	(2.9)	1	(3.2)
Total	38	(100.0)	35	(100.0)	31	(100.0)

Source : MNHN, Paris

TABLE 3. Morphological variations of mandibular molar teeth.

Dental Trait	M^1		M^2		M^3	
grade	n	(%)	n	(%)	n	(%)
Groove Pattern						
Y	23	(92.0)	12	(32.4)	3	(11.1)
+	2	(8.0)	18	(48.6)	7	(25.9)
X	0	(0.0)	7	(18.9)	17	(63.0)
Total	25	(100.0)	37	(100.0)	27	(100.0)
Cusp Number						
6	7	(16.3)	0	(0.0)	2	(5.3)
5	32	(74.4)	3	(6.1)	24	(63.2)
4	4	(9.3)	46	(93.9)	11	(28.9)
3	0	(0.0)	0	(0.0)	1	(2.6)
Total	43	(100.0)	49	(100.0)	38	(100.0)
Entoconulid (C-6)						
0	34	(91.9)	44	(1.00)	33	(97.1)
1	3	(8.1)	0	(0.0)	1	(2.9)
Total	37	(100.0)	44	(100.0)	34	(100.0)
Metaconulid (C-7)						
0	36	(90.0)	43	(1.00)	35	(1.00)
1	4	(10.0)	0	(0.0)	0	(0.0)
Total	40	(100.0)	43	(100.0)	35	(100.0)

Source : MNHN, Paris

TABLE 4. Morphological Variations of Deciduous Teeth.

	Shovel Shape				Tuberculum Dentale		Circular Enamel Hypoplasia			
	dc^1		dc^2		dc		dc		dc	
grade	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)
0	3	(27.3)	4	(66.7)	1	(16.7)	20	(83.3)	11	(57.9)
1	6	(54.5)	0	(0.0)	3	(50.0)	4	(16.7)	8	(42.1)
2	2	(18.2)	2	(33.3)	2	(33.3)	—	—	—	—
Total	11	(100.0)	6	(100.0)	6	(100.0)	24	(100.0)	19	(100.0)

Carabelli's Trait (dm^2)		
grade	n	(%)
0	2	(18.2)
1-3	8	(72.7)
4-6	1	(9.1)
Total	11	(100.0)

Cusp Number					
	dm^1			dm^2	
grade	n	(%)	grade	n	(%)
2	3	(30.0)	3	1	(9.1)
3M	3	(30.0)	4	10	(90.9)
3H	2	(20.0)	—	—	—
4	2	(20.0)	—	—	—
Total	10	(100.0)	Total	11	(100.0)

Cusp Number				
	dm_1		dm_2	
grade	n	(%)	n	(%)
4	4	(40.0)	0	(0.0)
5	4	(40.0)	8	(72.7)
6	2	(20.0)	2	(18.2)
7	0	(0.0)	1	(9.1)
Total	10	(100.0)	11	(100.0)

dm_2 Variations						
	C-6		C-7		Protostylid	
0	8	(72.7)	10	(90.9)	5	(62.5)
1	3	(27.3)	1	(9.1)	3	(37.5)
Total	11	(100.0)	11	(100.0)	8	(100.0)

TABLE 5. Mean crown diameters of permanent teeth from Neolithic Mehrgarh (in mm).

	Mesiodistal					Buccolingual				
Tooth	$\bar{x}$	n	sd	min	max	$\bar{x}$	n	sd	min	max
MAXILLA										
I1	8.72	29	0.51	7.8	9.8	7.28	33	0.37	6.6	7.9
I2	7.12	31	0.43	6.3	8.5	6.68	34	0.39	5.6	7.5
C	7.75	37	0.34	6.9	8.4	8.41	37	0.49	7.5	9.8
Pm3	7.10	36	0.41	5.6	7.8	9.56	37	0.41	8.8	10.5
Pm4	6.86	32	0.37	6.0	7.4	9.50	34	0.52	8.7	10.6
M1	10.63	39	0.50	9.7	11.8	11.89	41	0.49	10.8	13.5
M2	9.94	38	0.48	8.7	11.1	11.81	38	0.58	10.7	13.1
M3	9.29	30	0.86	7.8	10.8	11.20	31	0.91	8.7	13.0
MANDIBLE										
I1	5.48	26	0.34	4.8	6.0	6.06	30	0.33	5.6	6.8
I2	6.12	31	0.33	5.3	6.7	6.40	34	0.29	5.8	7.1
C	6.82	36	0.38	5.8	7.6	7.68	38	0.53	6.6	9.3
Pm3	7.04	38	0.40	6.2	7.8	7.98	40	0.52	7.1	9.5
Pm4	7.17	39	0.46	6.2	8.1	8.44	42	0.52	7.4	9.5
M1	11.54	38	0.55	10.4	12.9	11.12	39	0.43	10.3	12.0
M2	10.88	41	0.63	9.6	12.6	10.49	40	0.50	9.4	11.9
M3	11.01	36	0.75	9.6	12.5	10.30	37	0.60	9.1	11.4

Source : MNHN, Paris

TABLE 6. Mean tooth crown diameters at Neolithic Mehrgarh.

		MAXILLA					MANDIBLE				
Tooth	Var	x̄	(n)	sd	min	max	x̄	(n)	sd	min	max
di 1	MD	7.06	(11)	0.40	6.60	7.70	4.48	(12)	0.48	3.20	5.10
	BL	5.54	(11)	0.17	5.30	5.85	4.26	(12)	0.24	3.90	4.70
	CA	39.17	(11)	2.95	34.98	45.05	19.03	(12)	2.21	15.04	23.46
di 2	MD	5.75	(13)	0.28	5.30	6.20	5.11	(10)	0.27	4.80	5.70
	BL	5.24	(13)	0.30	4.70	5.60	4.68	(10)	0.22	4.40	5.20
	CA	30.14	(13)	2.71	24.91	33.60	23.95	(10)	2.24	22.05	29.64
dc	MD	7.31	(14)	0.77	6.00	8.90	6.31	(11)	0.41	5.30	6.80
	BL	6.32	(14)	0.50	5.40	7.10	5.82	(11)	0.28	5.30	6.20
	CA	46.51	(14)	7.90	32.40	57.85	36.76	(11)	3.56	28.09	41.48
dm 1	MD	7.62	(13)	0.41	6.90	8.40	8.83	(12)	0.48	8.10	9.80
	BL	9.35	(13)	0.36	8.70	9.90	7.56	(12)	0.28	7.10	8.00
	CA	71.23	(13)	5.48	60.72	80.36	66.74	(12)	5.07	59.76	77.42
dm 2	MD	9.51	(14)	0.61	8.60	10.90	10.66	(10)	0.55	9.60	11.70
	BL	10.47	(14)	0.41	9.70	11.00	9.40	(10)	0.40	9.00	10.10
	CA	99.75	(14)	9.48	83.42	119.90	100.31	(10)	8.33	88.32	118.17
SUM	CA	286.80 mm²					246.79 mm²				

TABLE 7. Comparison of mean crown diameters (MD and BL) by Period (IA, IB) for Neolithic Mehrgarh (left side in mm). * 0.05 level of size.

	Mesiodistal								Buccolingual							
	Level IA				Level IB				Level 1A				Level IB			
Tooth	n	x	SD	SE	n	x	SD	SE	n	x	SD	SE	n	x	SD	SE
MAXILLA																
I1	5	8.74	0.72	0.32	18	8.69	0.46	0.11	8	7.31	0.32	0.11	19	7.26	0.36	0.08
I2	7	7.29	0.56	0.21	19	7.02	0.40	0.09	10	6.83	0.39	0.12	19	6.58	0.39	0.09
C	9	7.80	0.22	0.07	20	7.80	0.42	0.09	10	8.63	0.53	0.17	19	8.38	0.43	0.10
P3	10	7.09	0.29	0.09	19	7.17	0.36	0.08	11	9.53	0.45	0.13	19	9.53	0.30	0.07
P4	8	6.89	0.39	0.14	18	6.75	0.36	0.08	10	9.49	0.59	0.19	18	9.39	0.47	0.11
M1	14	10.81	0.55	0.15	19	10.59	0.48	0.11	14	11.96	0.59	0.16	21	11.89	0.45	0.10
M2	11	10.02	0.53	0.16	19	9.89	0.55	0.13	11	11.92	0.78	0.24	19	11.81	0.49	0.11
M3	9	9.10	0.71	0.24	16	9.46	0.89	0.22	10	10.93	1.026	0.33	16	11.48	0.84	0.21
MANDIBLE																
I1	6	5.73	0.23	0.10	13	5.43	0.30	0.08	6	6.08	0.44	0.18	16	6.06	0.36	0.09
I2	8	6.08	0.26	0.09	17	6.20	0.34	0.08	9	6.46	0.21	0.07	18	6.39	0.27	0.06
C	11	6.91	0.39	0.12	18	6.78	0.35	0.08	12	7.79	0.52	0.15	19	7.70	0.55	0.13
P3	11	7.12	0.34	0.10	19	6.99	0.40	0.09	12	8.04	0.64	0.19	20	8.00	0.40	0.09
P4	12	7.39	0.55	0.16	20	7.06	0.42	0.09	13	8.41	0.63	0.18	22	8.52	0.43	0.09
M1	11	11.85	0.51	0.15	19	11.50	0.52	0.12	12	11.23	0.40	0.12	19	11.10	0.43	0.09
M2	13	11.19	0.67	0.19	22	10.70	0.60	0.13	13	10.60	0.57	0.16	22	10.44	0.50	0.11
M3	11	11.07	0.91	0.28	19	11.03	0.77	0.18	12	10.35	0.63	0.18	19	10.34	0.63	0.15

Source : MNHN, Paris

TABLE 8. Mean cross-sectional crown area for Neolithic Mehrgarh (left side, mm^2).

MAXILLA	$\bar{x}$	(n)	SD	min	max
I1	63.63	28	6.50	53.46	74.88
I2	47.84	30	4.53	38.64	62.05
C	64.98	34	5.12	52.44	74.70
P3	67.98	35	6.15	49.28	78.75
P4	65.16	31	6.42	53.40	78.44
M1	126.69	38	10.16	110.00	159.30
M2	117.71	37	9.24	97.44	136.74
M3	104.72	29	16.83	69.60	139.10
MANDIBLE					
I1	33.23	23	3.20	26.88	40.12
I2	39.26	28	3.20	32.33	44.88
C	52.65	36	6.13	39.60	67.89
P3	56.46	37	5.94	44.02	69.35
P4	60.69	39	6.83	46.50	73.47
M1	128.85	37	9.36	109.20	151.20
M2	114.26	40	11.21	91.18	149.94
M3	113.71	36	13.73	89.18	135.00

Upper 658.71 + Lower 599.11 = 1257 mm^2

TABLE 9. Dental trait frequencies in prehistoric South Asian skeletal series.

		Mehrgarh		Inamgaon		Sarai Khola		Timargarha	
Dental trait	Tooth	f	(n)	f	(n)	f	(n)	f	(n)
Shovel shape	I^1	.107	(28)	.000	(24)	.000	(12)	.000	(7)
Median Lingual Ridge	I^1	.577	(26)	.560	(25)	.182	(11)	.375	(8)
Marginal Interruption	I^1	.000	(27)	.000	(25)	.100	(10)	.125	(8)
	I^2	.516	(38)	.350	(20)	.100	(10)	.571	(7)
Cingulum Variation	I^1	.182	(11)	.042	(24)	.091	(11)	.000	(7)
Hypocone Size	M^1	.833	(42)	.659	(41)	.710	(21)	.770	(22)
Carabelli's Trait	M^1	.260	(27)	.325	(40)	.380	(13)	.500	(18)
Metaconule (C-5)	M^1	.250	(28)	.146	(41)	.230	(13)	.200	(19)
Cusp Number	M_2	.061	(49)	.167	(24)	.000	(19)	.118	(17)
Deflecting Wrinkle	M_1	.250	(8)	.114	(35)	.000	(15)	.230	(13)
Entoconulid (C-6)	M_1	.081	(37)	.108	(37)	.059	(18)	.000	(22)
Metaconulid (C-7)	M_1	.100	(40)	.056	(36)	.053	(19)	.080	(24)
Protostylid	M_1	.053	(19)	.000	(37)	.000	(15)	.043	(23)

TABLE 10. Comparative morphology of South Asian deciduous teeth.

		Prehistoric				Living	
		Mehrgarh		Inamgaon		Jats	
Dental trait	Tooth	f	(n)	f	(n)	f	(n)
Shovel Shape	(di^3)	.182	(11)	.154	(39)	.139	(36)
Tuberculum dentale	(dc)	.883	(6)	—	—	.075	(80)
Carabelli's Trait	(dm^1)	.091	(11)	.088	(45)	.118	(306)
Canine breadth Index	(dc/di^3)	103.5	(11)	99.3	(19)	102.8	(84)
Cusp Number	(dm^1, 2)	.300	(10)	.381	(44)	—	—
Cusp Number	(dm^2, 4)	.909	(11)	.653	(46)	.523	(314)
Cusp Number	(dm_1, 5)	.400	(10)	.426	(47)	—	—
Cusp Number	(dm_2, 5)	.727	(11)	.803	(61)	.941	(322)
Entoconulid (C-6)	(dm_2)	.273	(11)	.180	(61)	.012	(322)
Metaconulid C-7)	(dm_2)	.091	(11)	.017	(60)	.000	(322)
Protostylid	(dm_2)	.375	(8)	.016	(61)	—	—

Source : MNHN, Paris

TABLE 11. Tooth size of prehistoric skeletal series from Southern Asia.

Site	Country	Cultural Association	TCA (mm^2)	MCA (mm^2)	Source
Niah Cave	Sarawak	Neolithic	1312	—	Brace & Vitzthum, 1984
Jericho (PPNB)	Israel	Neolithic	1277	703	Smith, 1970
Natufian	Israel	Epipaleolithic	1264	703	Smith, 1970
MEHRGARH (MR3)	PAKISTAN	NEOLITHIC	1257	706	Lukacs *et al.*, 1985
Jarmo	Iraq	Neolithic	1248	680	Dahlberg, 1960
Abou Gosh	Israel	Neolithic	1240	685	Arensburg *et al.*, 1978
Non Nok Tha	Thailand	Bronze	1224	681	Brace, 1978
Mahurijhari	India	Iron	1220	677	Lukacs, 1982
Inamgaon	India	Chalcolithic	1218	671	Lukacs, 1985
Ban Chiang	Thailand	Metal Age	1216	682	Pietruszewsky (ms)
Bellan Bandi Palassa	Sri Lanka	Mesolithic	1210	713	Kennedy, 1965
Timargarha	Pakistan	Iron Age	1173	642	Lukacs, 1983b
Jericho	Israel	Bronze	1120	613	Smith, 1970
Sarai Khola	Pakistan	Iron Age	1107	613	Lukacs, 1983b
Harappa	Pakistan	Bronze	—	606	Dutta, 1983
Burzahom	India	Neolithic	1017	560	Basu & Pal, 1980

TABLE 12. Mean crown areas for deciduous teeth of prehistoric and living South Asians (sexes pooled, in mm^2).

	Prehistoric samples									Living samples	
	Mehrgarh			Inamgaon			Timargarha			Gujarati Hindu[1]	
	$\bar{x}$	(n)	SD	$\bar{x}$	(n)	SD	$\bar{x}$	(n)	SD	$\bar{x}$	SD
MAXILLA											
I^1	39.17	(11)	2.95	36.13	(19)	3.89	34.21	(4)	3.39	34.20	3.93
I^2	30.14	(13)	2.71	27.99	(20)	3.64	26.45	(6)	3.66	26.11	3.35
C	46.51	(14)	7.90	40.26	(27)	5.45	40.06	(9)	5.37	40.72	4.89
M^1	71.23	(13)	5.48	67.68	(32)	5.89	68.95	(8)	7.41	64.57	7.11
M^2	99.75	(14)	9.48	95.13	(32)	11.00	87.86	(8)	5.74	91.15	9.69
Maxillary crown area	286.8			267.19 (6.84 %)[2]			257.53 (10.21 %)			256.75 (10.48 %)	
MANDIBLE											
I_1	19.03	(12)	2.21	17.74	(20)	1.90	14.88	(4)	2.67	15.84	1.81
I_2	23.95	(10)	2.24	21.81	(22)	2.62	20.61	(6)	3.20	20.32	2.41
C	36.76	(11)	3.56	31.62	(22)	3.83	32.51	(9)	3.62	32.24	3.52
M_1	66.74	(12)	5.07	62.21	(36)	6.37	58.10	(13)	5.95	59.80	6.96
M_2	100.31	(10)	8.33	97.34	(36)	10.16	90.44	(13)	7.36	91.13	9.59
Mandibular crown area	246.79			230.72 (6.51 %)			216.54 (12.26 %)			219.33 (11.13 %)	
Total crown area	533.59			497.91 (6.69 %)			474.07 (11.15 %)			476.08 (10.78 %)	

1 n = 100 for Gujarati Hindu sample.
2 percent smaller than Mehrgarh sample.

Source : MNHN, Paris

Source : MNHN, Paris

The Dental Variation of Yuman Speaking Groups in an American Southwest Context

G. R. SCOTT, S. STREET & A. A. DAHLBERG

ABSTRACT

Data on ten morphologic crown trait variables are reported for five Yuman speaking tribes in the American Southwest. Using trait frequencies to assess relative degrees of affinity, we find that two River Yuman groups, Quechan and Mohave, are the most closely related while the Paipai and Maricopa fail to show notable ties to any of the other samples. A small Havasupai sample was the most divergent of the five groups but ties were closer to Paipai and Maricopa than to Quechan-Mohave.

When contrasted to Uto-Aztecan, Athapaskan, and Zuni samples, the Yuman groups in general show closer affinities to one another than to members of other language families. There are, however, differences among the Yuman samples. The Quechan and Mohave tend to be generally distinct from non-Yumans, but the Paipai and Maricopa show trait frequencies that put their relationship between Quechan-Mohave and three Uto-Aztecan samples. Analysis at the level of language families also indicates Yuman speakers to be closer to Uto-Aztecans than to either Athapaskans or the Zuni.

With some noteworthy exceptions, patterns of relationships among Southwest Indian tribes as indicated by tooth crown morphology are consonant with other lines of evidence, especially linguistics, gene frequencies, and anthropometry. As it does now appear possible to use dental traits to discriminate among groups, even at low levels of population differentia-

RÉSUMÉ

Des données concernant dix caractères morphologiques variables de la couronne dentaire sont présentées pour cinq tribus parlant Yuman dans le Sud-Ouest américain. En utilisant les fréquences de caractéres pour établir des degrés relatifs d'affinités, il apparaît que deux groupes de la rivière Yuman, les Quechan et Mohave, sont le plus étroitement reliés, tandis que les Paipai et Maricopa ne montrent de lien notable avec aucun des autres échantillons. Un petit échantillonage Havasupai apparaît comme le plus divergent des cinq groupes, mais il se relie de plus près aux Papai et Maricopa qu'aux Quechan-Mohave.

Quand on les oppose à des échantillons Uto-Aztéques, Athapaskan et Zuni, les groupes Yuman montrent en général des affinités plus étroites les uns avec les autres qu'avec les membres des familles différentes du point de vue linguistique. Il y a cependant des différences entre les échantillons Yuman. Les Quechan et Mohave tendent à être généralement distincts des non-Yuman, mais les Paipai et Maricopa présentent une fréquence de caractères qui situe leurs affinités entre les échantillons Quechan-Mohave et les trois Uto-Aztèques. L'analyse au niveau des familles linguistiques indique également que les tribus parlant Yuman sont plus proches des Uto-Aztèques qu'elles ne le sont des Athapaskan et des Zuni.

Avec quelques exceptions notables, le schéma des relations entre les tribus indiennes du Sud-Ouest, telles qu'elles résultent de la morphologie de la couronne

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Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

tion, collaborative efforts between archaeologists and dental anthropologists could contribute substantially to a number of long-standing problems in the prehistory of the American Southwest.

dentaire, est concordant avec celui qui provient d'autres données, en particulier du langage, de la fréquence génique et de l'anthropométrie. Puisqu'il apparaît maintenant possible d'utiliser les caractères dentaires pour distinguer les groupes entre eux, même à un faible niveau de différentiation des populations, un effort de collaboration entre spécialistes d'archéologie et d'anthropométrie dentaire devrait contribuer efficacement à résoudre un certain nombre de vieux problèmes concernant la préhistoire du Sud-Ouest nord-américain.

Introduction

Since the late 19th century, native American groups in the Southwest U.S. have served as the focal point for intensive anthropological inquiry. Broadly based ethnographies on many specific tribal groups conducted during the first three decades of the twentieth century have served as a foundation for the more problem-oriented, topical studies of recent times. At the very least, archaeological efforts have kept pace with those of the ethnologists. Cultural chronologies are well developed for many areas of Arizona and New Mexico and archaeologists now focus attention on cultural ecology, systems analysis, and regional syntheses, as well as culture history per se. One general measure of the breadth and depth of ethnological and archaeological research in the Southwest is indicated by the fact that two volumes of the recent Handbook of North American Indians are devoted to this single culture area (Ortiz, 1979, 1983).

While physical anthropologists have also been active in the Southwest for the past 80 years, one would have to characterize their efforts as more uneven than those of other anthropologists. The work of Aleš Hrdlička (1908, 1935) during the early part of this century still represents the most intensive attempt to characterize the biological variation of living Southwest Indian populations. Of course, his research was conducted prior to the development of anthropological genetics so his characterizations were limited to anthropometry, and miscellaneous physiological observations. While Hrdlička's data were analyzed subsequently by more advanced analytical techniques (Spuhler, 1954; Hanna, 1962), no worker since that time has matched the breadth of his early surveys. Genetical studies undertaken largely since the 1950s have generally focused on one or a few groups. The work of Brown *et al.* (1958) represents one early attempt to characterize the blood group gene frequency variation among several Southwest groups (Hopi, Navajo, Pima, Apache, Yuma, Mohave, Maricopa). More recently, Matson *et al.* (1968) and Niswander and his colleagues (Niswander *et al.*, 1970; Workman & Niswander, 1970; Workman *et al.*, 1974) have provided genetic characterizations for the Pima, Maricopa, Papago, and Zuni populations. The Navajo and Apache have also been subjected to genetic surveys of varying intensity (Kraus & White, 1956; Gershowitz, 1959; Corcoran *et al.*, 1962). Despite the efforts of serological geneticists, full genetic profiles for many groups in the Southwest are still not available. This is due in part to the fact that many early studies were limited to analysis of the ABO, MN, and Rh systems while recent studies often focus on systems other than red blood cell antigens such as albumin variants (Johnston *et al.*, 1969), serum proteins (Brown & Johnson, 1970), HLA alleles (Williams *et al.*, 1981) or immunoglobin haplotypes (Williams *et al.*, 1985).

Due in large part to the efforts of A. A. and T. Dahlberg, C. G. Turner II, and D. H. Morris, the one biological system which approximates Hrdlička's early attempts to describe anthropometric variation is the dentition. The above workers have collected large samples (200 + individuals) of dental casts from living Pima, Papago, Hopi, and Navajo Indians with smaller samples from Quechan (Yuma), Mohave, Zuni, and San Carlos Apache. Dental morphological characterizations and within - and between - group analyses of these groups have been the subject of previous works (Scott, 1973; Scott & Dahlberg, 1982; Scott *et al.*, 1983). In terms of an even broader characterization of dental variation

Source : MNHN, Paris

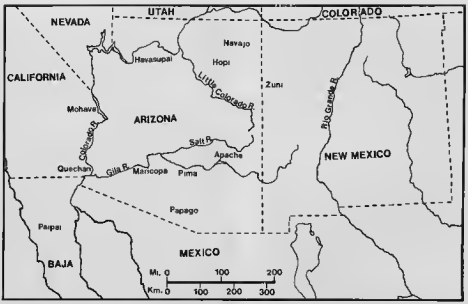

FIG. 1. — Map of the American Southwest which shows location of eleven tribal groups studied for morphologic tooth crown variation.

in the Southwest, the major gaps in the above studies are the lack of Keresan and Tanoan speaking Rio Grande Pueblo an samples (excluding the Tewa sample from the Hopi mesas) and a better representation of River and Upland Yuman groups. While the absence of Rio Grande Pueblo-an data remains, it is now possible to expand the representation of Yuman speaking groups with the addition of Paipai, Maricopa, and Havasupai samples. This study will thus focus on the analysis of dental variation within five Yuman speaking groups (Quechan and Mohave in addition to the above three groups) and comparisons with Uto-Aztecans, Athapaskans, and the Zuni, as described previously. The geographic distribution of the eleven Southwest groups considered is shown in Fig. 1.

MATERIAL AND METHOD

A. *Samples*

Background information on the three Yuman samples is provided in the following descriptions:

PAIPAI

Despite their linguistic affiliation with other Yuman groups, the Paipai of Baja California actually fall outside the area of the Greater Southwest. It has been proposed, however, that this is an artifact of a recent migration from the northeast with the Paipai possibly derived from a Yavapai antecedent (Winter, 1967). Nevertheless, contemporary Paipai consider an area of northern Baja, stretching from the Colorado River through the Sierra de Juarez to the Pacific Ocean south of Santo Tomas, to be their historical homeland. This is reflected in recently collected oral testimony and traditional stories (Hinton & Watahomegie, 1984).

Regardless of their origin, the Paipai have frequently interacted with other Yuman groups of Baja California (e.g. the Tipai and Ipai). Their alliance with the Cocopa of the Colorado River delta to help counter the powerful Quechan (Yuma)-Mohave alliance is also frequently noted (Kroeber, 1920; Gifford, 1933; Gifford & Lowie, 1928). Interestingly, despite their geographic proximity to Delta and River Yuman groups, the Paipai are linguistically allied with Upland (or Arizona) Yuman groups (Yavapai, Walapai, Havasupai). This curious fact has been noted by several investigators concerned with the origins of "Proto-Yuman", linguistically (Kroeber, 1943; Winter, 1967; Massey, 1949). In contrast to their linguistic affinities, the material culture of the Paipai is more closely related to that of their

Source : MNHN, Paris

immediate neighbors such as the Cocopa, Tipai, and Ipai (Gifford, 1933; Drucker, 1941).

In the 1950s, during an ethnographic survey of the Paipai, Roger Owen and Ernst Goldschmidt obtained impressions and made permanent casts of 54 Paipai dentitions. These casts were then sent to A. A. Dahlberg for inclusion in his major collection of Southwest Indian dentitions and are described here for the first time.

Maricopa

Linguistically, Maricopa is closely related to members of the River Yuman group, especially the Mohave and Quechan (Yuma). The Maricopa now reside on the Gila River in central Arizona (Harwell & Kelly, 1983), but they are thought by some to have once occupied a geographical position on the Colorado River between the Quechan and Mohave populations until extensive warfare with these two groups forced them to move to their present location (Forbes, 1965). The Maricopa were traditionally allied with the Pima, Cocopa, and Halchidhoma, and even secured trade goods from the Paipai through these channels (Spier, 1933). Today, the presence of the Maricopa in central Arizona is somewhat obscured by their position adjacent to the much larger Pima Indian population.

During their three decades of study of the Pima Indians, the Dahlbergs collected several thousand dental casts. Within the context of this work, a smaller sampling of the Maricopa tribe was carried out. For this study, 43 Maricopa dental casts have been observed.

Havasupai

The Havasupai traditionally occupied a large territory on the Coconino plateau, south of the Grand Canyon from the Colorado River on the west to the Little Colorado River in the east (Schwartz, 1983). Since the encroachment of other populations in the mid-20th century, the Havasupai have been restricted to the lower drainages of Cataract Creek Canyon, a small side branch of the Grand Canyon. Culturally and linguistically, the Havasupai are most closely related to the Walapai. Archaeological evidence suggests that both groups descended from early populations in the same general area and have been allies in recent times to face such groups as the Yavapai (Heizer & Whipple, 1971). These three Pai groups are all classified as Upland Yuman (Kendall, 1983).

In 1969, the senior author obtained a small series of Havasupai impressions/casts during a brief excursion to Havasu village. Unfortunately, the sample numbers only 12 individuals.

In addition to the three Yuman groups outlined above, dental data are also available for the Quechan (n = 73) and Mohave (n = 52) populations. The Quechan and Mohave are related both linguistically and culturally, sharing many common elements of material culture and kinship recognition (Bee, 1973). As noted earlier, the Mohave and Quechan commonly served as allies during their almost constant warfare against other Yuman neighbors along the Colorado River. These samples have been described in earlier papers (Scott & Dahlberg, 1982; Scott *et al.*, 1983), although the sample referred to as Quechan was previously called Yuma. Quechan is now the preferred name for this tribal grouping and the change also eliminates confusion between a single sample and the broader language family.

While analysis will initially center on the dental variation among the five Yuman speaking groups, they will also be compared to other Southwest Indian groups. These include the Uto-Aztecan speaking Pima, Papago, and Hopi, the Athapaskan speaking Navajo and Apache, and the linguistically distinct Zuni. Frequency data for these samples can be found in earlier publications (Scott, 1973; Scott & Dahlberg, 1982; Scott *et al.*, 1983), but it should be noted that the subpopulations of both Hopi and Navajo have been combined to form single samples in the present analysis.

B. *Crown traits*

The suite of morphologic crown traits utilized in this study includes the following (with abbreviation and observed tooth in parentheses): Bilateral Winging (WING; UI1), Canine Tubercle (CTUB; UC), Carabelli's Trait (CARA; UM1), Metaconule (META; UM1), Distal Accessory Ridge (DAR; LC), Multiple Lingual Cusps (MLC; LP2), Hypoconulid (LHYP; LM2), Cusp 6 (C6; LM1), Cusp 7 (C7; LM1), and the Protostylid (PROT; LM1). More detailed descriptions and the trait

Source : MNHN, Paris

classifications used for these features can be found in Scott & Dahlberg (1982) and Scott *et al.* (1983). In contrast to these prior studies, shoveling (UI1) and the hypocone (UM1), which are basically invariant (100 %) features in Southwest groups, are not included in the analysis.

Although trait expression was always scored on a ranked scale for each antimere, analytical emphasis is placed on total crown trait frequencies. These frequencies are considered the best single indicator of the genotypic distributions which underly the class frequency distributions of these threshold (Falconer, 1960) or quasicontinuous traits (Grüneberg, 1952). While right and left antimeres were always observed, the individual count method was utilized to maximize sample size (Turner & Scott, 1977; Scott, 1980). In all instances male and female trait frequencies were combined for analysis. All dental variables were scored by a single observer (G.R.S.) to eliminate the potential for interobserver error.

C. *Analysis*

The primary purpose of this study is to assess relative degrees of similarity among Yuman and other Southwest Indian groups using total crown trait frequencies for ten morphologic variables. Toward this end, we have employed the method of Harpending & Jenkins (1973) which involves the calculation of coefficients of kinship, the derivation of relationship matrices, and the extraction of eigenvectors and eigenvalues through a principal components analysis of relationship matrices. This latter set of calculations allows the extraction of the greatest amount of variance in the total data set that can be attributed to a few primary components. Moreover, when the eigenvectors are rescaled to reflect the varying magnitudes of the eigenvalues, it is possible to plot the first two or three eigenvectors to give a visual representation of relative between-group affinity. Although all methods have limitations, this type of graphical representation is less arbitrary than cluster analysis which can be performed in a number of substantially different ways.

Although the methods of computation are described in detail in Harpending & Jenkins (1973) and are summarized in Scott *et al.* (1983), certain points should be made about the assumptions involved and key characteristics of the relationship matrices. First, this method assumes that all populations under study shared a common ancestor at some point in time so that the mean trait frequency for all groups is the best estimate available for the common ancestral frequency. All between-group variation is then measured relative to these presumed ancestral frequencies. Secondly, the traits analyzed are assumed to be independent of one another. Third, genetic drift is assumed to be the primary mechanism that has generated the differences between groups. This latter assumption is standard for almost all distance measures, and the method employed here shares with these other measures the inherent inability to sort out population convergence brought about by gene flow.

Regarding the relationship matrix, two important points should be made. First, the trace of the matrix shows calculated values which indicate the relative level of differentiation of one group from the total variation among all groups. A small value in the trace thus indicates that a sample is relatively undifferentiated from the expected ancestral population frequencies. A large value in the trace indicates a group is highly divergent from ancestral frequencies. In the relationship matrix, every group also shows a pairwise distance value to every other sample included in the analysis. Unlike most distance matrices, however, in which large values indicate dissimilarity and small values similarity, the opposite holds true for matrices derived from kinship coefficients. In these matrices, both positive and negative values are possible (in fact, each row and each column sum in a symmetrical matrix equals zero) with the largest positive value indicating the greatest amount of similarity and the largest negative value indicating the greatest between group difference. These characteristics are emphasized because of the major differences between this method and other biological distances estimates.

Results

Table 1 presents the total crown trait frequencies and associated sample size per variable for the five Yuman groups. In addition, summary

Source : MNHN, Paris

measures for Yumans are provided for each trait by both actual count for combined samples and unweighted means and variances. These summary measures are usually quite similar, but an exceptionally high cusp 6 frequency in the small Havasupai sample does have the effect of elevating the unweighted mean by eight percent above the actual count. As a characterization of Yuman groups would not differ substantively from those already given for Southwest Indians in general (Scott & Dahlberg, 1982), their dental variation will be discussed in the context of other Southwest samples. Data on these additional samples are presented in Table 2 by both individual tribal group and linguistic family. Three Uto-Aztecan, two Athapaskan, and one Zuni sample are thus available for comparison to Yumans.

In a comparison of trait frequencies in the first two tables, Zuni is often an outlier, so Yuman variation is characterized primarily in terms of the relationship to Uto-Aztecan and Athapaskan ranges. For winging, while the frequency range for Yuman is greater, their mean frequency is close to that for Uto-Aztecans and somewhat higher than for Athapaskans. For the canine tubercle and Carabelli's trait, Yuman and Uto-Aztecan means are again similar, with Athapaskan frequencies higher for the canine tubercle and lower for Carabelli's trait. The metaconule, by contrast, shows similar frequencies for Uto-Aztecans and Athapaskans with Yumans having lower frequencies. For the lower canine distal accessory ridge, Uto-Aztecans and Athapaskans differ significantly while the Yuman mean falls between these two groupings and has a range that essentially overlaps both. For lower second premolar multiple lingual cusps, the Yuman range is exceptionally narrow and the mean trait frequency exceeds that of both Uto-Aztecans and Athapaskans. The lower second molar hypoconulid frequency tends to be lower in the Yuman samples but this is distorted somewhat by a very high frequency in the small Havasupai sample. A similar effect is evident in cusp 6 frequencies. Uto-Aztecans and Athapaskans show narrow cusp 6 frequency ranges around 45-50 % while the Yuman range is consistently below these frequencies except for the Havasupai. For cusp 7, Yumans exhibit frequencies similar to Uto-Aztecans, but above those of Athapaskans. Finally, Yumans have slightly but not significantly lower frequencies for the protostylid than do either Uto-Aztecans or Athapaskans.

A relationship matrix among the five Yuman samples is presented in Table 3. The trace of the matrix reveals that the Paipai are the least differentiated of these groups. On a group by group basis, this matrix reveals that the Mohave is by far the most similar group to the Quechan followed by the Paipai and much more distantly by the Maricopa and Havasupai. Considering the Mohave, their greatest similarity is to Quechan, then Maricopa, Paipai, and Havasupai. The Paipai are not strongly divergent from any of the samples, but they are closest to the Quechan, then the Mohave, Maricopa, and Havasupai. The Maricopa, like the Paipai, are not strongly divergent from any group, but they are most similar to the Mohave, followed by the Paipai, Havasupai, and Quechan. Finally, the small Havasupai sample is strongly divergent from all other Yuman groups but, on a relative basis, they are much closer to the Paipai and Maricopa than they are to either the Quechan or Mohave. To show these relationships graphically, a plot of the first two rescaled eigenvectors is presented in Fig. 2.

The next step in the analysis is the consideration of Yuman variation in a broader Southwest context. This involves the computation of a relationship matrix among four Yuman samples (the small Havasupai sample is excluded here), the Pima, Papago, Hopi, Navajo, Apache, and Zuni. This matrix is shown in Table 4.

Considering first the Quechan, their closest relationship is to the Mohave with more distant affinity to the Navajo, Apache, and Paipai. The three Uto-Aztecan samples are consistently divergent from the Quechan as are the Maricopa. In contrast to the Quechan, the Mohave consistently show their greatest degree of affinity to the other three Yuman groups (in order, Quechan, Maricopa, Paipai) and are quite divergent from all Uto-Aztecan and Athapaskan samples. The Paipai again show a relatively low level of divergence from all other samples with the lowest value (.016) in the trace of the matrix. Despite this, the highest positive values associated with the Paipai are, in order, the Mohave, Quechan, Maricopa, Navajo, and Papago samples. Except for the Zuni, no group is markedly divergent from the Paipai. As for the Maricopa, their closest relationship is with the Mohave and

Source : MNHN, Paris

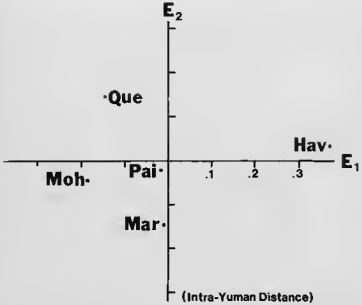

FIG. 2. — Plot of first two rescaled eigenvectors indicating relative degrees of affinity among five Yuman speaking samples.

Papago followed by the Papai and Pima. They are about equally divergent from the Hopi, Navajo, Apache, and Quechan.

Although the distance matrix is revealing, an eigenvector map can also be constructed to show graphically the relationships among these ten Southwest Indian samples. The first three eigenvectors are presented in Table 5. These account for 82 % of the total variation among all groups. The first eigenvector sets the four Yuman samples and Zuni apart from all Uto-Aztecan and Athapaskan samples. The second eigenvector serves to divide two Yuman groups (Mohave and Maricopa), two Uto-Aztecan groups (Pima and Papago), and Zuni from the two Athapaskan groups (Navajo and Apache), two Yuman groups (Quechan and Paipai), and the Hopi.

The first two eigenvectors are plotted in Fig. 3. The resulting map illustrates a number of interesting points. First, the close placement of the Pima to the Papago and the Navajo to the Apache both indicate the degree of similarity possible with this method. In contrast to these close relationships, all four Yuman samples are scattered fairly broadly on the right side of the map with no two groups exceptionally close. The Quechan and Mohave are the most divergent of the Yuman samples while the Paipai and Maricopa are plotted on points between Quechan-Mohave on the one hand and the three Uto-Aztecan samples on the other.

On a broader level, the mean trait frequencies for the five Yuman samples, the three Uto-Aztecan samples, the two Athapaskan samples, and the single Zuni sample were subjected to a parallel analysis with the resulting relationship matrix shown in Table 6. This matrix reveals that among these four language families, the closest ties are between Uto-Aztecans and Yumans. Athapaskans are about equally divergent from both groups while the Zuni stand consistently apart from all other groups.

DISCUSSION

To what extent do the patterns of relationship derived from tooth crown morphology correspond to other types of evidence. This question will first be addressed for the five Yuman samples, followed by a discussion of Yuman and non-Yuman affinities.

The Quechan and Mohave tribes are, by all accounts, culturally and linguistically allied. An analysis of anthropometric variation provides the strongest evidence that the affinity between these two groups has a biological component (Hanna, 1962). Unfortunately, there are insufficient genetic data to assess this relationship further. The third River Yuman group, the

Source : MNHN, Paris

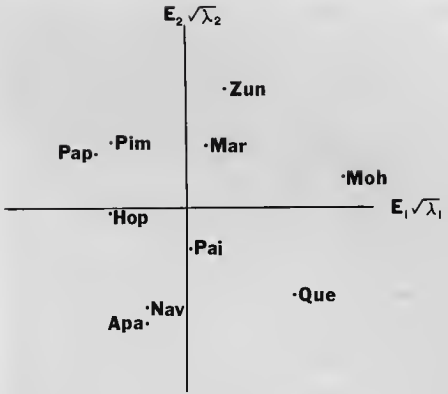

FIG. 3. — Plot of first two rescaled eigenvectors indicating relative degrees of affinity among ten Southwest Indian samples.

Maricopa, are closest to the Mohave and are most distantly removed from the Quechan. Based on the anthropometric analysis of Hanna (1962), Maricopa should be about equally distant from Quechan and Mohave. Again, genetic data cannot resolve this fully although the limited data available for the ABO and Rh systems show similar frequencies for the Quechan and Maricopa. The Paipai provide us with a particularly interesting paradox. We are unaware of any other biological data on this group so there is no way to assess their pattern of relationships in this manner. Somewhat suprisingly, considering the fact they reside on the fringe of the broader Yuman geographic distribution, the Paipai are the most generalized of all Yuman groups. They are not particularly close nor distant from any other Yuman group. The Havasupai, closer linguistically to the Paipai than to the River Yumans, show the highest level of differentiation from the other four Yuman groups. This is probably a function of small sample size, at least in part. It is perhaps revealing, however, that the Havasupai are markedly distinct from Quechan-Mohave and about equidistant from Maricopa and Paipai. Genetic data on the Havasupai (Merbs, 1962) and Maricopa (Matson *et al.*, 1968) show that these groups share in common an absence of the A and B alleles in the ABO system, relatively low frequencies of M (60-65 %), and a similar ratio of the R1 and R2 alleles in the Rh system. Overall, the relationships found among this set of Yuman groups are generally consistent with other lines of evidence; unfortunately, this evidence does not include complete genetic profiles which would provide a much better standard for assessment.

Considering the overall pattern of relationships among the ten Southwest Indian groups studied (Fig. 2), several points can be made. First, there is a substantial body of genetic data to support the close affinity of Pima and Papago (Matson *et al.*, 1968; Workman & Niswander, 1970; Williams *et al.*, 1985). This is further corroborated by anthropometric similarity (Hanna, 1962). The consensus among linguists is that Pima and Papago diverged from a common ancestor only four to five centuries ago. In other words, dental morphologic data are entirely consistent with other evidence which supports

Source : MNHN, Paris

close ties between Pima and Papago. Close affinity between the two southern Athapaskan groups, Navajo and Apache, is also indicated not only by dental morphology but by linguistics (Hale & Harris, 1979) and genetic data (Brown *et al.*, 1958; Williams *et al.*, 1985). Genetically, the A allele at the ABO locus has long been noted as setting southern Athapaskans apart from other Southwest groups. The frequency of the A allele in Navajo and Apache is typically in the range of 15-20 % whereas it ranges between 0 and 10 % in other groups. An additional genetic marker which is clearly reflective of their common ancestry is the presence of albumin Naskapi which is found almost exclusively in Athapaskan and Algonkin groups in the New World (Lampl & Blumberg, 1979). Interestingly, the observance of the albumin Naskapi phenotype in a non-Athapaskan group in the Southwest is unequivocal evidence of Athapaskan admixture. On the other hand, another rare albumin variant, albumin Mexico, is found in low frequencies among many Mesoamerican groups and most Southwest Indian tribes (e.g. Pima, Papago, Zuni, Cocopa, Maricopa) (Lampl & Blumberg, 1979), but is absent among all northern Indian and Eskimo populations. The presence of this allele in Navajo and Apache also indicates admixture with non-Athapaskan populations in the Southwest. The occurence of albumin Mexico in Apache (26/641; q = .020) and Navajo (10/755; q = .007) samples and the extreme rarity of albumin Naskapi in non-Athapaskans (3/3553; q = .0004) suggests that gene flow is largely unidirectional (i.e. non-Athapaskan to Athapaskan). The three individuals who did exhibit albumin Naskapi phenotypes came from three different small samples: Hopi, Mohave, and Maricopa. Thus there is evidence for at least some gene exchange between Yumans and Athapaskans.

The Hopi and Zuni, although both viewed culturally as western Puebloans, are linguistically quite distinct. The Hopi are classified in the Shoshonean (or Northern) branch of Uto-Aztecan while the Zuni language has proved so distinctive that it cannot be clearly linked to any other Southwest or North American Indian language family (Hale & Harris, 1979). One distance analysis which utilized four Gm haplotype and Km allele frequencies found the Hopi to be most closely allied with Papago, Pima, and Zuni and consistently distinct from Apache, Navajo, and the Walapai. Zuni's closest affinities were shown to be with Papago, Hopi, Pima and Walapai while distance values with four Athapaskan samples were notably larger. While a full serological profile is not available for the Hopi, such a profile is available for the Zuni (Workman *et al.*, 1974). Although they were the most dissimilar group among those compared (Pima, Papago, Maricopa), the Zuni did not prove to be distinctive for any particular genetic system. They did, however, have a B frequency of 5 % which is only notable in that this allele is completely lacking in almost all other Southwest groups. Brown & Johnson (1970) also report an unusually high frequency of the Hp1 allele in Zuni compared to other Southwest groups while their frequencies for three other serum proteins were not distinctive. Finally, the presence of albinism in Hopi and Zuni and its essential absence in other tribes (Hrdlička, 1908) has long been thought to indicate affinity or intermarriage between these two groups. Despite these various indicators, the dentition does not clearly reveal a close relationship between Hopi and Zuni. Groups showing closest affinity to the Hopi are the Pima and Papago, but there is also some link to the Navajo and Apache (see Fig. 3). Dentally, the Zuni are the most divergent group of the ten samples. While they are not strongly allied with any other single group, they are closest to the Mohave, Pima, Hopi, and Apache.

Of the four Yuman groups, a relatively complete serological profile is available only for the Maricopa (Matson *et al.*, 1968). As an accessory analysis to determine the degree to which blood group gene frequencies and tooth crown traits correspond in showing patterns of relationship, we analyzed separately the six samples (MAR, PIM, PAP, ZUN, NAV, APA) for which relatively good genetic data are available using both blood group and crown trait frequencies. The plots of the first two eigenvectors are shown individually for the blood group and dental analyses in Fig. 4. A visual inspection of the two graphs reveals a close correspondence in relative between group affinities when measured by independent genetic and dental data sets. Each system indicates: (1) a close relationship between the Pima, Papago, and Maricopa; (2) similarity between the Navajo and Apache and their distance from other groups; and (3) the relative distinctiveness of Zuni. It should be noted that

Source : MNHN, Paris

we used all the alleles that were available for all seven samples (i.e. no estimation or selection was involved), there was no manipulation of the dental data, such as the omission of certain traits, and the eigenvector maps are drawn to exactly the same scale.

Lacking other types of biological data, interpreting the relationships of the Paipai based on the dentition will remain a dilemma. While the Paipai are most similar to other Yuman groups, this does not obviate the fact that they are not much further removed from all Uto-Aztecan and Athapaskan groups. They contrast in a significant way only with Zuni. The most parsimonious explanation of the Paipai would hold that they are a composite group involving primarily Yuman and Uto-Aztecan components. This question, however, requires further study.

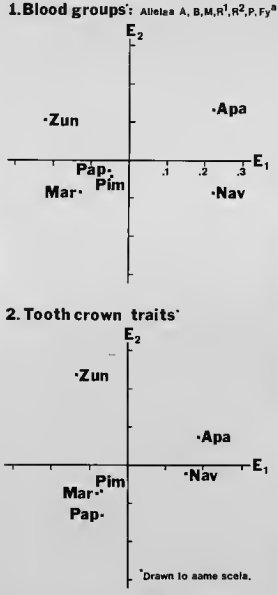

FIG. 4. — Plot of first two rescaled eigenvectors for six Southwest Indian groups based on (1) blood group gene frequencies and (2) tooth crown-trait frequencies.

One question that remains is why we have gone to such lengths in this work and earlier studies to assess relative degrees of similarity among Southwest Indian populations. In other words, what is the value of such research that can be characterized as neither functional nor adaptational in approach. Quite simply, it is our view that within the broader context of physical and dental anthropology, there is a place for historical science. The utility of tooth crown morphology in studies of recent human populations would be quite circumscribed if not applied to problems of population history. In this regard, teeth have an obvious advantage over the simple genetic markers in the blood: they can be observed among both the living and the dead. Why then did we begin with the study of living populations rather than skeletal samples? The availability of dental casts from several thousand individuals might appear to be the unstated reason, but this number could be matched or exceeded by the skeletons recovered in archaeological contexts in the Southwest. The primary reason relates to one aspect of the methodology of historical science; that is, argue from the known to the unknown. With living populations, there are subsidiary data which help us assess whether or not measures of affinity derived from crown trait frequencies are consistent with other lines of evidence. Examples include levels of diversity within language families, blood group and serum protein frequencies, dermatoglyphics, anthropometrics, and other biological traits that reflect underlying genotypic variation. Moreover, gene exchange with adjacent or distant populations can often be obtained through oral testimony. Cultural similarities are probably the least useful because of the high potential for convergence when unrelated groups inhabit similar biotic provinces. Still, culture traits, including oral histories, can sometimes prove to be useful supplements in understanding the distributions and interrelationships of different human groups.

To complete an overview of the dental mor-

Source : MNHN, Paris

phological variation in the Southwest, several avenues of potential research immediately present themselves. For example, one of the most outstanding areas historically and archaeologically is the Rio Grande Valley of central New Mexico. This area supports the highest density of contemporary Puebloan groups and is also accessible to study by the anthropologist. It is clear from a perusal of the literature that little biological data have been collected from these communities.

With the foregoing in mind, the next step in a dental survey of Southwest groups should involve the collection of dental casts from Keresan and Tanoan speaking groups in New Mexico. This would encompass at least twelve contemporary Pueblos surrounding the Rio Grande and its tributaries and two or three further to the west. It is quite possible that these groups are distinctly different from Yumans, Uto-Aztecans, and Athapaskans as indicated by the small and quite diverse samples which have previously been analyzed from Zuni and Tewa (Scott & Dahlberg, 1982). Once accomplished, this broad characterization of Southwest dental variation would provide us with an opportunity to examine skeletal material from different regions and times and test specific hypotheses concerning migrations and inferred relationships developed by archaeologists.

These possibilities should draw immediate attention from archaeologists in the Southwest where conflicting interpretations of population movement and fissioning still play a major role in the assessment of cultural phenomena. It is still not clear, for example, whether people from the Colorado Plateau (Mesa Verde) did actually eclipse groups within the San Juan Basin during the 14th century. The need for further skeletal research to address this problem has been noted by Southwest archaeologists (cf. Cordell, 1984), but dental data would probably be even more useful since teeth show less environmental plasticity than skeletal characters and can also be studied in living populations. Contemporary dental data would also shed a great deal of light on later population movements into the Rio Grande Valley.

With a robust data base on modern groups, many controversies relating to the proposed ancestral-descendant relationships of the Hohokam, Mogollon, Hakataya, and Anasazi could be addressed. How were the bearers of these cultural traditions actually related to one another? Do they reflect affinities with Uto-Aztecans, Yumans, Keresans, Tanoans, or none of the above? It will only be by a careful consideration of population history interpreted from morphological similarities, coupled with archaeological analysis, that these problems can be systematically addressed. A more broadly based anthropological approach with cooperation among archaeologists, skeletal biologists, and dental anthropologists may be the key to understanding many past and present trends in the movements and relationships of extinct and extant groups in the Southwest. The American Southwest, as one of many culture areas around the globe, should continue to serve as a valuable test case for the role of dental morphology in unraveling problems of origins and relationships.

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Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Total tooth crown trait frequencies for Yuman samples.

Trait	Yuman samples					Total count	Mean [1]	Variance [1]
	PAI	MAR	HAV	QUE	MOH			
WING	.381	.433	.417	.182	.327	.312	.348	.0103
	(42)	(30)	(12)	(66)	(49)	(199)		
CTUB	.590	.563	.750	.622	.684	.626	.642	.0057
	(39)	(16)	(12)	(37)	(19)	(123)		
CARA	.714	.600	.818	.762	.723	.714	.723	.0064
	(49)	(40)	(11)	(63)	(47)	(210)		
META	.200	.057	.182	.125	.068	.120	.126	.0042
	(45)	(35)	(11)	(56)	(44)	(191)		
DAR	.558	.733	.600	.434	.650	.547	.595	.0124
	(43)	(15)	(10)	(57)	(25)	(150)		
MLC	.261	.318	.273	.286	.308	.286	.289	.0006
	(46)	(22)	(11)	(49)	(26)	(154)		
LHYP	.643	.611	.917	.473	.533	.602	.635	.0292
	(42)	(18)	(12)	(36)	(15)	(123)		
C6	.357	.417	.778	.279	.098	.306	.386	.0625
	(42)	(36)	(9)	(68)	(41)	(196)		
C7	.209	.256	.400	.182	.268	.229	.263	.0071
	(43)	(39)	(10)	(66)	(41)	(195)		
PROT	.244	.289	.375	.324	.250	.287	.296	.0030
	(41)	(38)	(8)	(68)	(40)	(195)		

[1] Unweighted mean and variance.

TABLE 2. Total tooth crown trait frequencies for Uto-Aztecans, Athapaskans, and Zuni (adapted from Scott & Dahlberg, 1982; Scott *et al.*, 1983).

Trait	Uto-Aztecan			Mean [1]	Athapaskan		Mean [1]	Zuñian
	PIM	PAP	HOP		NAV	APA		ZUN
WING	.382	.353	.314	.350	.239	.172	.206	.200
	(1103)	(170)	(277)		(431)	(29)		(60)
CTUB	.636	.529	.737	.634	.656	.737	.697	.909
	(695)	(153)	(236)		(305)	(19)		(11)
CARA	.726	.719	.803	.749	.613	.583	.598	.745
	(1242)	(160)	(279)		(434)	(48)		(47)
META	.199	.222	.189	.203	.212	.154	.183	.029
	(970)	(126)	(180)		(339)	(39)		(34)
DAR	.687	.746	.596	.676	.436	.500	.468	.790
	(803)	(158)	(208)		(291)	(18)		(15)
MLC	.194	.252	.154	.200	.235	.174	.205	.304
	(992)	(179)	(260)		(340)	(23)		(23)
LHYP	.705	.700	.763	.723	.714	.632	.673	.571
	(662)	(141)	(194)		(252)	(19)		(7)
C6	.459	.526	.498	.494	.445	.562	.504	.452
	(1144)	(135)	(215)		(362)	(48)		(42)
C7	.346	.335	.246	.309	.184	.082	.133	.222
	(1247)	(158)	(277)		(414)	(49)		(60)
PROT	.448	.351	.344	.381	.357	.292	.325	.575
	(1086)	(137)	(241)		(375)	(48)		(40)

[1] Unweighted means.

Source : MNHN, Paris

TABLE 3. Symmetrical relationship matrix for Yuman samples.

	QUE	MOH	PAI	MAR	HAV
QUE	.044	.017	.003	-.017	-.047
MOH	.017	.046	-.002	.002	-.063
PAI	.003	-.002	.011	-.004	-.008
MAR	-.017	.002	-.004	.027	-.009
HAV	-.047	-.063	-.008	-.009	.126

TABLE 4. Symmetrical relationship matrix for Yuman, Uto-Aztecan, Athapaskan, and Zuni samples (excluding Havasupai).

	QUE	MOH	PAI	MAR	PIM	PAP	HOP	NAV	APA	ZUN
QUE	.044 [1]	.022	.005	-.013	-.023	-.025	-.015	.007	.006	-.008
MOH	.022	.058 [1]	.007	.012	-.014	-.019	-.021	-.019	-.027	.000
PAI	.005	.007	.016 [1]	.004	-.002	.003	-.001	.004	-.005	-.032
MAR	-.013	.012	.004	.035 [1]	.002	.011	-.015	-.015	-.015	-.006
PIM	-.023	-.014	-.002	.002	.025 [1]	.023	.012	-.005	-.017	-.001
PAP	-.025	-.019	.003	.011	.023	.036 [1]	.007	-.006	-.016	-.014
HOP	-.015	-.021	-.001	-.015	.012	.007	.024 [1]	.005	.005	-.001
NAV	.007	-.019	.004	-.015	-.005	-.006	.005	.027 [1]	.023	-.020
APA	.006	-.027	-.005	-.015	-.017	-.016	.005	.023	.048 [1]	-.002
ZUN	-.008	.000	-.032	-.006	.001	-.014	-.001	-.020	-.002	.083 [1]

1 Values in trace of matrix indicating overall level of differentiation from mean of all groups.

TABLE 5. First three eigenvectors derived from kinship matrix for 10 samples accounting for 82.1 % of variance among groups.

Eigen-vectors	% of variance	QUE	MOH	PAI	MAR	PIM	PAP	HOP	NAV	APA	ZUN
1st	28.8	.146	.214	.006	.027	-.103	-126	-.107	-.056	-.054	.052
2nd	27.5	-.116	.044	-.052	.088	.090	.081	-.006	-.135	-.156	.161
3rd	25.8	.010	-.074	-.105	-.093	-.036	-.091	.027	.016	.112	.233

TABLE 6. Symmetrical relationship matrix among language families (based on mean trait frequencies) in the American Southwest.

	YUM	UAZ	ATH	ZUN
YUM	.014	.005	-.002	-.017
UAZ	.005	.020	-.006	-.019
ATH	-.002	-.006	.031	-.024
ZUN	-.017	-.019	-.024	.060

Source : MNHN, Paris

Source : MNHN, Paris

Variation in the Dentition

A. A. DAHLBERG

ABSTRACT

The sites of occurrence and the nature and causes of variations in size, form and structure of the teeth are many and of considerable diversity of relevance. Patterns of occurrence are mostly orderly and respond to environmental insults and gene interactions. Mutations and chromosomal aberrations can and do influence genotypes or phenotypes that can recapitulate ancestral forms that are interpretive problems posed against variants of ontogenetic or other related insults. A wide range of variants are useful in ethnic and other anthropological biological problems.

RÉSUMÉ

Les points d'apparition, comme la nature et les causes, des variations dentaires portant sur la taille, la forme et la structure, sont nombreux et très variés dans leur signification. Leur distribution est le plus souvent ordonnée et répond à des agressions du milieu et aux interactions des gènes. Les mutations et les aberrations chromosomiques peuvent influencer — et influencent — les génotypes ou les phénotypes susceptibles de récapituler les formes ancestrales ; elles posent ainsi des problèmes d'interprétation du fait des variations dues à des agressions intervenant en particulier au cours de l'ontogénèse. Un grand nombre de variations dentaires peuvent être utilisées pour résoudre des problèmes d'ethnologie et d'anthropologie biologique.

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Source : MNHN, Paris

Variations in form, size and structure of teeth range widely and have a high priority in biological studies. They have been useful in pursuing investigations of the processes of evolutionary selection, growth, development and genetics of the dentition. Variation is found in greater or lesser intensities and in wide distribution of frequencies, responding differently to a long list of environmental and developmental insults. Bateson (1894) observed that teeth generally follow a pattern of greater variation at the beginning and ends of repeated structural series, a pattern that occurs in digits, bones, ribs, muscles, corolla of flowers, et cetera. This pattern frequently matches with many of the last added structural modifications in the evolutionary sequences. In man and in other primates, there is a division of the tooth rows into tooth groups, viz., incisors, canines, premolars and molars. Within each group the anterior member is as a rule the more stable tooth morphologically compared to the others that are prone to decrease in size or ancestral form (lateral incisor, second premolar, and second and third molars).

The limitations of sites of variation are generally well adhered to, but bulges, pits, ridges and cusps can appear on surfaces of teeth where they are not usually expected. Occasionally a maldesigned cusp (Fig. 1) will appear obtrusively on an occlusal surface where fast-wearing abrasive action or a sharp functional clash will cause breakage and exposure of the vital pulp tissue, not planned for in the established architecture of the tooth.

Many variations are small in size and extent but yet amenable to statistical measurements and procedures for population studies. An example of this might be the single furrow category of Carabelli's Cusp (Fig. 2) on the antero-lingual aspect of upper molars (Chart 1). In some instances, the furrow continues occlusally over the edge and, in joining the groove of the fovea, gives the impression of an extra cusp. Another example could be a groove on the mid lingual surface of lower molars, running occlusally over the lingual line angle between the two lingual cusps and effectively producing a cusplet sometimes assumed to be the " 7th " cusp (Fig. 3). In some groups, such cusplets have been reported in as high as 15 or more percent for the first permanent molars with lesser frequency percentages on the second and third molars.

Gradients in size or absence of the distalmost cusp (hypoconulid) on the disto-buccal end of the occlusal surfaces of lower first permanent molars or lower deciduous second molars presents cusp-groove patterns of Y5 or Y4 configuration (Fig. 3). The cusp-groove pattern generally is

FIG. 1. — Permanent teeth with prominent protoconid cusps are seen high above the other cusps and occlusal plane. Also note the unusually high central lobe of the canine (lobodontia).

Source : MNHN, Paris

FIG. 2. — A furrow category of the Carabellis's Cusp on the anterolingual surface of an upper molar tooth is seen extending over the occlusal edge and joining the groove of the fovea.

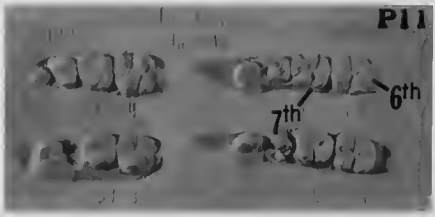

FIG. 3. — The 6th and 7th cusps are seen on the occlusal surface of the lower molar. The lower left cast shows a marked reduction of the hypocones on both the deciduous second molar and the first permanent molar, contrasting sharply with the strongly portrayed hypocones on the upper left cast. Likewise, the concept of morphological fields is illustrated on the lower right cast where the hypoconulid is expressed prominently on the deciduous second molar, and is absent on the usually very stable and conservative first permanent molar.

accompanied by further reduction on the other permanent molar occlusal surfaces to Y4 or + 5 on the second and to a Y4 or + 5 on the third. A less frequent and not as great a size decrease of the entoconid (disto-lingual cusp) is sometimes found on lower molars. These decreases in cusp sizes are accompanied by increases or change in the associated cusps and relative locations of grooves. The protoconid generally enlarges in mesio-distal measurement which in turn shifts the bucco-occlusal groove between the buccal cusps distally, thereby changing the pattern category to the " + ". In man, many populations have a Y5 pattern for the lower first molars, Y4, + 5 or + 4 for the second and a + 4 for the third. One of the exceptions to the sequences in the field concept theory occurs in the frequent loss of the hypoconulid in the second molar and the large presence of that cusp on the 1st and 3rd molars. The deciduous second molars retain the ancestral pattern even more than the permanent first molar. In Fig. 3 there is a reduced form on the first permanent molar with a more fully expressed cusp-groove pattern

Source : MNHN, Paris

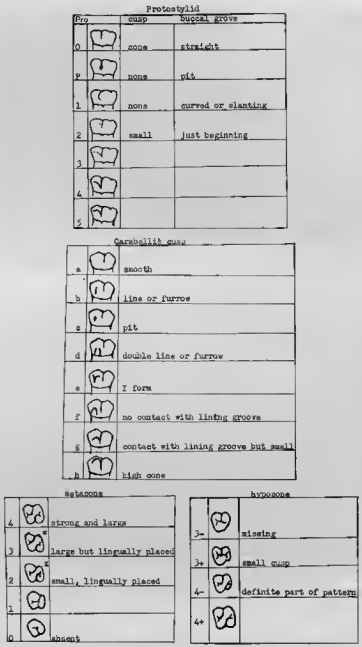

CHART. 1. — Class distinctions of four of the most commonly used traits of the dentition.

on the second deciduous molars. Additionally to cusp groove pattern variations on the occlusal surfaces there is another group of variations which has not been given much attention. These variations involve the waning terminal activity of ameloblasts of developing cusps and their wandering trails of enamel in the central pits and fissures of occlusal surfaces. The deflecting wrinkle (Fig. 4) is a good representative of this group. It originates as a strong ridge bucally from the mesiolingual cusp and turns distally rather abruptly, sometimes crossed by a groove. It extends in any direction available, especially when the central fossa has not been filled in by termination of the other cusps. The tail of the wrinkle, on occasion, extends over and beyond

Source : MNHN, Paris

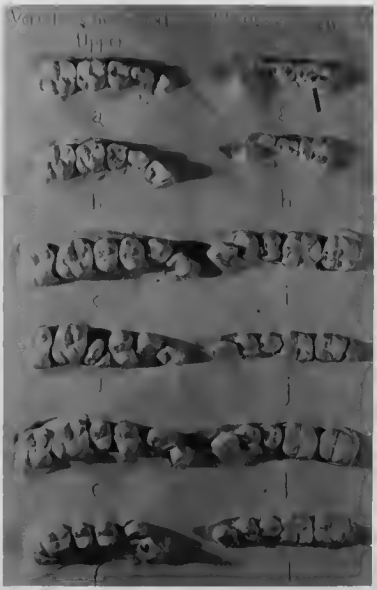

FIG. 4. — The Tooth Trait Plaque of the Dahlberg-Zoller series which illustrates the variations in proportions of posterior premolars and molars. Casts " G " and " J " show the possible terminations and general conformation of the deflecting wrinkle of lower first molars.

the central fossa aspect of the other cusps. The second molar deflecting wrinkle varies frequently by a limitation to the single initially bucally located surface and is confined to the mesiolingual cusp.

Traits can be confused with secondary effects of the environment and interactions of many sorts. One special condition reported from time to time is that which involves enamel formation and structure. It has been particularly troublesome, causing confusion because of difficulty in analysis and the problem of developmental insults sustained at very early ages *in vitro*. Many excellent studies and reviews have been published in recent years, too numerous to repeat here, by Sarnat, Schour, Pindborg, Kraus, Fisher, Korenhof, Molnor, Tobias, Bradlow, Armelagos, Johanson, Brothwell, Mayhall, Cook, Buikstra, McHenry and a host of others. A great deal of attention in the literature has been directed

Source : MNHN, Paris

toward the problem of a triad of symptoms known as Hutchinson's Triad of Congenital Syphilis.

Robert Mann of the Anthropology Department of the University of Tennessee sought opinions recently about the teeth of the upper and lower jaws (Figs. 5 and 6) of an American Indian child of about 4 years of age recovered from the Edgehill archaeological site located in Charles City, Virginia. The dating of the ossuary contents was between AD 1300 and 1400 and the operation was conducted by Professor N. F. Barkas, aided by his students of the Williams and Mary College in Virginia Department of Anthropology.

The importance of the specimen stems from the fact that it has most of the deciduous teeth well preserved and *in situ* with the unerupted but

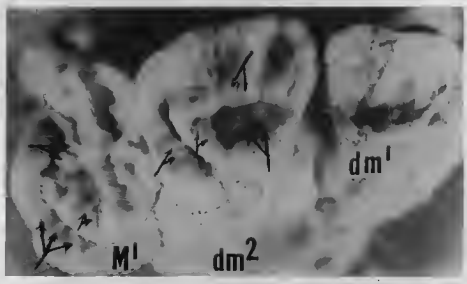

FIG. 5. — Occlusal view of maxillary first and second deciduous molars of the William and Mary Amerind dentition illustrating disproportionately large buccolingual dimension and the disparate growth activity of the enamel islands of the coronal occlusal morphology. Note twin and triplet islands and the deep occlusal areas of the fossae.

FIG. 6. — Occlusal view of the mandibular first and second deciduous molars of the William and Mary specimen with the same observations plus the even greater kidney shape of the occlusal surfaces.

Source : MNHN, Paris

visible first permanent molars present and intact. The deciduous molars and the permanent first molars are of an unfamiliar coronal dimension and design witb what seems to be a disorganized surface of small ridges and islands of enamel (Fig. 7). The disorganized enamel structure is confined to the occlusal surface with a smooth normal appearance of the buccal, labial and lingual surfaces. The disorganized enamel islands at first sight appear to coincide with descriptions of the mulberry molars (Hutchinson).

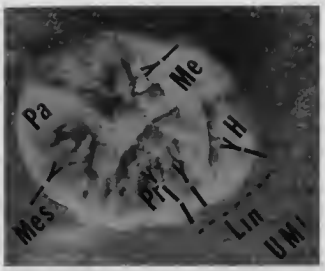

FIG. 7. — Enlarged surface view of the upper first permanent molar showing the islands in more detail.

Several features of this specimen suggest strong similarities to the orangutan deciduous dentitions. This is seen particularly in the shape, size and details of the posterior teeth. Both the upper and lower posterior deciduous teeth have a much greater talonid width measurement buccolingually than the trigonid measurement. A deep central fossa in the distal part of the occlusal surface is very large and prominent in the second deciduous molars. However, most other details are strictly hominid. The enamel islands have a definite design plan. The basic initiation and alignment of the epithelial cells is a clear indication of the direction and development of the ameloblast activity. It resulted in a straight bucco-occlusal margin and development of the ameloblast with erupted ameloblast performance gingivally on the buccal surface. To the lingual, the growth and subsequent calcification was variously interrupted and reactivated. It is observed that the ridges and islands are frequently doubled or tripled. The deciduous upper incisor pulp chambers are large and a few have apical divisions into double root formation at the terminal three millimeter band. The double root and enlarged pulp chambers have been observed in a few other high inbreeding Amerind groups. The William and Mary mandible, maxilla and teeth are the subject of another more detailed paper in preparation.

Several workers, Black, Zsigmondy and others, have raised objection to the tendency of some reports of years ago to associate enamel dysplasias too closely to treponemal infections. Fossils of the past give evidence of some ameloblastic dysplasias with some on the third molars (Tobias, 1986). Fisher (1986, in press) points to evidence of treponematosis back in Palaeolithic times.

Variability remains a broad spectrum of biological and dentition studies.

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Source : MNHN, Paris

Docodont Molars as Tribosphenic Analogues (Mammalia, Jurassic)

P. M. BUTLER

ABSTRACT

The convergence of *Docodon* to therian mammals, with its possession of a " protocone " on upper molars and a " metaconid " on lower molars, has led in the past to mistaken views of its relationships. Comparison of molar occlusion between docodonts and lepticti-ids shows that there was much functional parallelism, due to the development in both of a crushing function, performed by a cusp arising from the lingual cingu-lum. This parallelism was superimposed on an earlier divergence, when the molars were purely shearing structures. The common ancestor had occlusal relations like *Megazostrodon*, not *Morganucodon*. The chewing movement of *Docodon* was less transverse than in typical therians, and the power stroke was directed slightly posteriorly.

RÉSUMÉ

La convergence de *Docodon* avec les Mammifères thériens, reflétée dans la présence d'un « protocone » aux molaires supérieures et d'un « métaconide » aux molaires inférieures, a conduit dans le passé à des vues erronées sur les affinités de ce genre. La comparaison de l'occlusion des molaires chez les docodontes et les lepticti-des montre un important parallélisme fonction-nel, dû au développement dans les deux cas d'une fonction d'écrasement, réalisée par un tubercule émané du bourrelet lingual. Ce parallélisme s'est surimposé à une divergence plus ancienne, alors que les molaires étaient des structures purement coupantes. L'ancêtre commun avait des relations occlusales identiques à celles de *Megazostrodon* et non de *Morganucodon*. Le mouvement masticatoire de *Docodon* était moins transversal que celui des thériens typiques, et le « power stroke » était dirigé légèrement vers l'arrière.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris*, (série C) **53** : 329-340.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

In 1939 I wrote a paper on the teeth of Jurassic mammals, in which I showed that, except in multituberculates, the dentition is organized in the same way as in modern mammals, if allowance is made for differences in molar cusp pattern and in the number of teeth. I homologized molar cusps by the way in which they changed when traced from tooth to tooth along the series, and I concluded that, of the three main cusps of the tritubercular upper molar, the protocone was absent in all the known Jurassic mammals, with the exception of *Docodon*. At that time *Docodon* was classified in the order Pantotheria, family Docodontidae (Simpson, 1929). Most pantotheres belong to the family Dryolestidae, in which the lingual cusp of upper molars is not the protocone but a lingually situated paracone; the buccal part of the molar is occupied by a series of stylar cusps. In docodonts the paracone, and also the metacone, are buccal in position, and the stylar cusps are represented only by a cingulum.

I postulated (Butler, 1941) that the tritubercular molar had been derived from one in which the paracone and metacone were in a median position, having stylar cusps like dryolestids in combination with a protocone, thus being intermediate between the two families of pantotheres. The discovery in the Middle Cretaceous of tribosphenic teeth (Patterson, 1956), later called *Pappotherium* and *Holoclemensia*, which had this structure, appeared to confirm the theory. In most later mammals the stylar cusps have been reduced to a cingulum, and I suggested that in some phyletic lines they may never have been present, so that a tritubercular pattern might have come directly from a docodont pattern. I cited as a possible case the Late Cretaceous-Early Tertiary family Leptictidae.

We now know that *Docodon* is far removed from the ancestry of tribosphenic mammals. It is not a pantothere, and its "protocone" is an entirely independent development from the protocone of tribosphenic molars. Nevertheless it is of interest as an example of convergence. Resemblance between two unrelated animals usually means that both have become adapted to similar function, and the comparison of convergent structures may help us to understand their function. In the present case the function is chewing; I will therefore compare the adaptations to chewing in docodont molars with those in molars of tribosphenic origin. As examples of the latter I will use leptictid molars, which resemble those of docodonts particularly closely, but much of what I have to say would apply to tribosphenic molars in general.

Observations

A. *Morphological comparison of docodonts with leptictids*

A distinction may be drawn between shared characters that were derived from a common ancestor and are therefore homologous, and analogous characters that arose independently, by convergence. The last common ancestor of docodonts and leptictids was probably Late Triassic in age, and perhaps related to *Megazostrodon* (Crompton, 1974). As in other early mammals, the molars of both jaws would be elongated anteroposteriorly and supported by two roots; the cusp pattern would be triconodont, with three main cusps placed in line (Crompton & Jenkins, 1968). Cingula, probably bearing minor cuspules, would be present on the lingual side of the lower molar and on both sides of the upper molar. This ancestral pattern has been modified in different ways in docodonts and leptictids, but some of its features have been retained in both (Fig. 1).

On the upper molars, the buccal cusps of docodonts are homologous with the paracone and metacone of leptictids, being derived from cusps A and C of early mammals (nomenclature of Crompton & Jenkins, 1968). Cusp B is absent in docodonts; in leptictids it is probably represented by the parastyle (Butler, 1978). The lingual part of the upper molar is a greatly extended lingual cingulum, but the extension has taken place independently in the evolution of docodonts and leptictids. In both cases there is a lingual root, probably produced by subdivision of the posterior root of the ancestral molar. The protocone-analogue of docodonts is called cusp X by Krusat (1980). Posterior to it is a small cusp Y at the lingual end of a cingulum; this is the hypocone-analogue. The protocone is V-

Source : MNHN, Paris

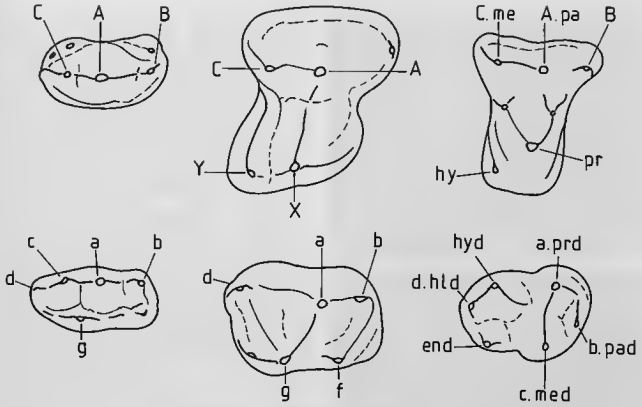

FIG. 1. — Right upper and left lower molars of *Megazostrodon* (left), *Docodon* (centre) and *Leptictis* (right), showing cusp homologies.

shaped in leptictids, with a preprotocrista and a somewhat lower postprotocrista; in docodonts there is only one transverse crest, which could be considered as the analogue of the preprotocrista.

In both families the highest cusp on the lower molars is the protoconid (cusp a of early mammals); it is situated buccally. The anterior cusp (b) is also buccal in docodonts, but on leptictid molars it is displaced lingually, as the paraconid; however on dP_4 it remains in a buccal position. Cusp c is absent or rudimentary on docodont molars, though retained on the premolars where it is posterior to the protoconid. In leptictids it is the metaconid, on the lingual side of the tooth opposite the protoconid. This lingual displacement of the metaconid goes back to *Kuehneotherium*, and it is characteristic of all therian mammals. The protoconid-metaconid crest (in therians called the protocristid) has rotated from a longitudinal to a transverse direction. Analogous to the metaconid in docodonts is cusp g, an elevation of the lingual cingulum present in early mammals such as *Morganucodon* and *Megazostrodon*; Parrington (1967) called it the kuehnecone. In docodonts it is connected with the protoconid by a crest that is analogous with the protocristid. Anterior to cusp g is cusp f, also developed from the lingual cingulum. This is connected by a crest with the anterior buccal cusp (b). It can be regarded as the analogue of the leptictid paraconid. The posterior part of the lower molar, forming the talonid in leptictids, is very poorly developed in docodonts. They have nothing corresponding to the hypoconid or entoconid, but a small posterior cusp (d) is probably homologous with the hypoconulid. Posterior to the metaconid-analogue there is a supplementary cusp which occupies a similar position to the entoconid, but its occlusal relations are more like the metastylid that occurs in some ungulates and primates, though not in leptictids.

B. *Chewing movements*

In early mammals the lower teeth passed upwards and medially to the upper teeth, so that

Source : MNHN, Paris

the buccal surface of the lower teeth was in contact with the lingual surface of the upper teeth, and food was cut as upper and lower crests passed each other like the blades of scissors. There was no opposition between the teeth; at the end of the stroke the highest cusps of the lower molars were received in pits in the maxilla. In tribosphenic mammals, and also in docodonts, the upward movement was terminated by lower molars biting against the lingual extensions of upper molars, so that food could be crushed. The teeth were then in centric occlusion. The upward movement into centric occlusion had a transverse (medial) component, owing to the inclination of the occluding surfaces from the vertical, and the lower teeth continued to move medially as the jaw began to open, the crushing surfaces gliding past each other. A second set of attrition facets was thus produced, on the lingual surface of the lower buccal cusps and the buccal surface of the upper lingual cusps. These are the lingual-phase facets of Mills (1955). Ridges on the occluding surfaces may have had some grinding effect, but the primary function of the lingual phase was probably to carry crushed food towards the tongue (Fig. 6).

Jenkins (1969) gave a detailed description of the facets of *Docodon*, but he did not distinguish between those produced during jaw closure and during jaw opening. He noted that nearly all the facets were steeply inclined, and therefore the transverse component of the chewing movement was small. Nevertheless, the presence of facets both on the buccal and the lingual surfaces of the lower buccal cusps implies movement in two directions, i.e. up and down. It also implies that the lower buccal cusps could move transversely by a distance equal to the width of the basins of the upper molars (Fig. 2). Transverse movement of the jaw may have been restricted, as Jenkins suggested, by the transverse process of the pterygoid bone of the skull. In leptictids the transverse component was much greater, for the upward movement was inclined at about 45° to

FIG. 2. — *Docodon victor*, YPM 11826, C-M_3, lateral view. Straight lines indicate the direction of the closing stroke.
Below (left), relation of lower and upper molars during closure.
Below (right), relations of molars as seen in anterior or posterior view (lingual to the right); closing phase, centric position, opening phase.

Source : MNHN, Paris

the vertical, and the lingual-phase movement approached the horizontal. Docodonts lack an angular process on the mandible for insertion of an internal pterygoid muscle, which in living mammals is an important factor in transverse jaw movement (Hiiemae & Crompton, 1985; Crompton, 1985). However, docodonts do possess a pseudangular process, situated more anteriorly, and near this Krusat (1980) found in *Haldanodon* a muscle scar for what he tentatively interpreted as a ventral part of the temporalis. Such a muscle could pull the jaw medially during chewing.

The transversely rounded dorsal surface of the condyle and the low, unfused symphysis of *Docodon* suggest that rotation of the mandible round its axis may have played a part in mastication (Crompton & Ai-Lin Sun, 1985). In *Didelphis* the teeth are tilted more medially during jaw closure and more laterally during jaw opening. If there were such a change of tilt between the buccal and lingual phases of occlusion, the angle between the two sets of facets would be greater on upper teeth than on lower teeth. Associated upper and lower teeth are not available in *Docodon*, but to judge from unassociated specimens the angular difference seems to be small.

In *Tenrec* (Oran & Crompton, 1986) axial rotation of the jaw takes place during the buccal phase (the lingual phase is nonexistent in this insectivore), and it accounts for the transverse movement of the lower molars across the uppers, movements of the jaw being impeded by the upper canines (Mills, 1966). An analogous mechanism has been proposed to explain the wear of the Early Jurassic mammal *Dinnetherium* (Jenkins *et al.*, 1983), in which a facet produced by the tip of cusp a is less steeply inclined than facets formed later in the chewing stroke. Crompton & Ai-Lin Sun (1985) noted a similar but less marked mode of wear in *Moganucodon*. A specimen of *Morganucodon* at Cambridge (Eo Mx 30) shows it very clearly (Figs. 3 and 4). On M^3 a deep notch, due to lower cusp a, has been worn involving cusps A and B; it has a less steep inclination than the wear facets on the lingual cingulum. On M^2 cusp B has been removed and the wear surface continues to cingulum level, again with an increase of slope. Cusp B of M^1 shows only the steep type of wear, on its lingual surface. A number of other specimens show this sort of

FIG. 3. — Above, scanning electron micrographs of *Docodon victor*, left M_1-M_4, and M_3 at higher magnification, to show striations on the lateral face of the anterior cusp. From a cast.
Below, *Morganucodon*, right M^1-M^4, to show wear facets. Cambridge University Museum of Zoology Eo Mx 30.

Source : MNHN, Paris

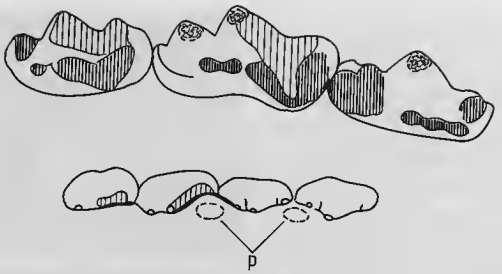

FIG. 4. — *Morganucodon*, Cambridge University Museum of Zoology, Eo Mx 30.
Above, right M^2-M^4, showing steep (closer shading) and more horizontal facets.
Below, M^1-M^4 as seen parallel to the steep facets; p = pits in the maxilla for reception of cusps a of M_2 and M_3.

wear to a lesser degree, e.g. M^2 of Eo Mx 23 and Eo Mx 33. On some lower molars cusp c is worn in a similar way, against upper cusp A. Rotation of the jaw is not the only possible explanation. The surfaces that first make contact with the highest cusp of the opposing teeth might be subject to greater wear, including abrasion due to puncture-crushing, and so they would become more horizontal. Alternatively (or in addition) inaccurate occlusion might result in a degree of medial slipping of the teeth into a position where they can occlude in a normal manner. I have not observed wear of this type in *Docodon*, in which cusps B and c are rudimentary or absent. Facets on the edge of crests, such as 1b and 4a of Jenkins (1969) are probably due to abrasion.

Jenkins (1969) apparently, from his figure 4C, D, thought that the closing phase had a forward component in *Docodon*, as is usual in mammals. Gingerich (1973) however noted from striations that the closing movement was somewhat backwardly directed, and he assumed that the teeth could be closed together from two different directions. This seems improbable. Backwardly oblique striations do occur on the buccal facets of cusps a and b in YPM 11826 (Figs. 2 and 3), and I have also seen backwardly oblique striations on a lower molar of *Haldanodon*. In YPM 11826 the lower canine has a facet, high on its anterior surface, due to contact with the last upper incisor; this facet is inclined backwards dorsally, approximately parallel to the striations on the molars.

The chewing stroke was backwardly inclined in traversodontid cynodonts (Crompton, 1972), and it is horizontally backward in tritylodonts and multituberculates (Krause, 1982); there is also a backward component in *Ornithorhynchus* (Hopson & Crompton, 1969). Kemp (1982) estimated that in advanced cynodonts the bite force against the lower cheek teeth was orientated forwards and downwards, and in broad-toothed forms the most effective bite occurred when the lower tooth pressed posterodorsally against the upper tooth. This may have been the case in docodonts. In leptictids the chewing movement was slightly forwards, probably due to an anteromedial movement of the condyle.

Jenkins (1969) believed that some anteroposterior movement was possible in *Docodon*. He noted that a facet (17a) on the lower tooth apparently occluded with two facets (2 and 6) on the upper tooth, one more posterior than the other. A more likely explanation is that 17a occluded with the two upper facets successively as the lower tooth travelled lingually in the lingual phase. 17a is extended obliquely to the probable direction of motion; in centric occlusion it contacts facet 6, but as the molar moved lingually it occluded with the more posterior facet 2 (Fig. 5).

Source : MNHN, Paris

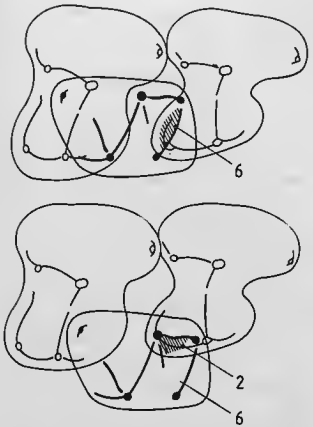

FIG. 5. — *Docodon*, a lower molar superimposed on two upper molars, in centric position (above) and at the end of the lingual phase (below), to show how facets 2 and 6 could be produced successively during the opening movement.

C. *Intercuspal occlusal relations* (Fig. 6)

Although the upper buccal cusps of docodonts are homologous with the paracone and metacone of leptictids, their occlusal relations are different. In both groups the protoconid passed up anteriorly to the paracone, to reach the embrasure between two upper teeth, but whereas in leptictids an anterior crest (paracrista) of the paracone sheared against the buccal part of the protocristid, in docodonts the anterior surface of the paracone is not crested, and though a facet is formed against the posterior surface of the protoconid there was no cutting action between the two cusps. The protoconid has a strong anterior crest that connects with the paraconid (cusp b). This crest shears against the paracone-metacone crest of the more anterior upper molar. In leptictids (except on dP_4) the anterior protoconid crest reaches only to the metacone; it is continuous at its anterior end with the transverse crest (paracristid) that ends at the paraconid. The paracone-metacone notch occludes with the hypoconid of the corresponding lower molar. However, on dP_4 the paraconid shears between the paracone and metacone of dP^3 in place of the hypoconid of dP_3, which is undeveloped.

In tribosphenic molars, including those of leptictids, the crests of the protocone also have a shearing function: the preprotocrista against the metaconid (i.e. the lingual part of the protocristid) and the postprotocrista against the entoconid. In *Docodon* an anterior crest from the protocone-analogue shears with a posterior crest from the metaconid-analogue, but these crests are longitudinal, whereas the preprotocrista and protocristid of leptictids are transverse. The docodont analogues of the preprotocrista and protocristid do not have a shearing function, perhaps because the transverse chewing movement is more restricted than in tribosphenic mammals. Even the longitudinal shear between the lingual cusps seems to be a late development in docodont evolution, as it is hardly present in *Haldanodon*.

In centric occlusion each lower molar makes

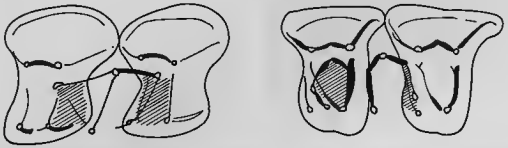

FIG. 6. — *Docodon* and *Lepticti*s in centric occlusion. Heavy lines represent shearing edges, shaded areas represent crushing surfaces.

Source : MNHN, Paris

contact with two adjacent upper molars. Thus there are two crushing areas, a posterior one against the corresponding upper molar, and an anterior one against the more anterior upper molar. The posterior area in leptictids is the lingual surface of the hypoconid, which meets the buccal surface of the protocone. In docodonts it is the posterior surface of the protocristid-analogue, which meets the anterior surface of the preprotocrista-analogue. In leptictids the crushing surface faces somewhat posteriorly on the upper molar, the preprotocrista being more strongly developed (i.e. more ventral) than the postprotocrista. In docodonts the crushing surface faces forwards on the upper molar; it is anterior to the preprotocrista-analogue, whereas in leptictids it is posterior to the preprotocrista. This difference may reflect the different directions of the upward jaw movement: slightly forward in leptictids, slightly backward in docodonts.

The anterior contact surface is small in leptictids. The paraconid and its buccal ridge (paracristid) meet the hypocone and the posterior cingulum of the more anterior upper molar. In docodonts, in a similar manner, cusp f, cusp b, and the ridge connecting them are in contact with the hypocone-analogue and associated cingulum.

As the jaw begins to open in the lingual phase, the opposing surfaces slide past each other. In leptictids the hypoconid passes across the protocone, and the paracristid glides along the posterior cingulum. In *Docodon*, movement between the posterior contact surfaces produces facet wear on the posterolingual face of the protoconid (cusp a) (facet 11a of Jenkins, 1969) and on the oblique ridge between cusps g and d (11b), against the anterior surface of the preprotocrista-analogue (20b) and the edge of the anterior crest of the protocone-analogue (19c). Facets related to the anterior contact surface are on the lingual side of cusp b (facet 6) and the anterolingual side of cusp a (2), against the posterior side of the preprotocrista-analogue (17c, 17d). Minor crests, which cross during the movement, would concentrate pressure at their crossing-points and provide a milling function; for example, the oblique crest from cusp g crosses the posterior crest of the protocone-analogue. Fluting of the slopes of the cusps, characteristic of docodonts, would have the same effect. In leptictids the crests of the hypoconid cross those of the protocone.

Interpretation

The relationship between *Docodon* and *Morganucodon* has been recognised since Kühne (1950). The wide difference between their molar patterns was partly bridged by the discovery of the earlier docodonts *Haldanodon* (Krusat, 1980) and *Borealestes* (Waldman & Savage, 1972). Crompton & Jenkins (1968) analysed the changes that would be involved in the evolution of a docodont from *Morganucodon*. Subsequently Crompton (1974) pointed out a number of resemblances to *Megazostrodon*, though this has some derived characters, such as the enlarged external cingulum of the upper molars, which probably exclude it from docodont ancestry. Crompton suggested that docodonts had not been derived directly from *Morganucodon* or *Megazostrodon* but from an unknown related form.

Megazostrodon differs from *Morganucodon* in the occlusal relations between upper and lower cusps (Fig. 7). In *Morganucodon*, lower cusp a occludes between upper cusps A and B, and the lower cusp occluding between A and C is c; in *Megazostrodon*, lower cusp a occludes anteriorly to B, and the cusp between A and C is lower cusp b of the following tooth. In this respect *Morganucodon* resembles *Triconodon* while *Megazostrodon* resembles *Kuehneotherium* (Crompton, 1974). Upper cusp B is missing in docodonts, so its relations to a are unknown. However, the cusp that bites between A and C is not c, but b, as in *Megazostrodon*. Cusp c is retained on docodont premolars, and in USNM 2707 it can be traced back to the molars as a minor elevation low on the posterior side of a (Fig. 8). It would thus be anterior to the tip of A when the jaws closed, again as in *Megazostrodon*. Thus the ancestry of docodonts seems to be nearer to *Megazostrodon* than to *Morganucodon*.

Such an ancestry would require only minor modification of the hypothesis of Crompton & Jenkins (1968) regarding the course of molar evolution. A widened cingulum, lingual to upper cusp A, would meet the crest of the lower tooth,

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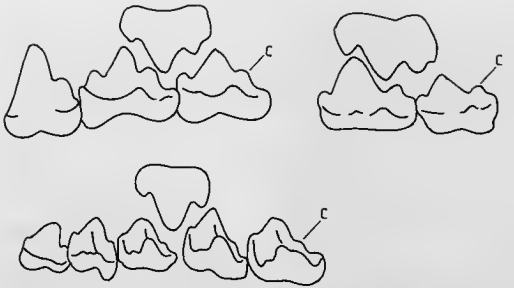

FIG. 7. — Relation of upper and lower molar cusps of *Megazostrodon* (above, left), *Morganucodon* (above, right) and *Docodon* (below); anterior end is to the left. In *Megazostrodon* the highest cusp of the upper molar bites behind lower cusp c; in *Morganucodon* it bites anterior to c; in *Docodon* c is rudimentary, but the relations resemble *Megazostrodon*. *Docodon* drawn from USNM 2707.

forming a crushing surface. This contact would be situated near the posterior end of the lower molar, behind cusp c. Its enlargement would involve development of the protocone-analogue and elimination of cusp c. The cingulum would extend in a posterolingual direction, progressively overlapping the lower molar, so that the crushing surface would reach the posterior face of cusp g, which was presumably already present. The extension would also overlap the anterior part of the more posterior lower molar, developing contact with cusps b and f. The lingual lower cusps f and g appear to have been primitively related to the notches between the buccal cusps. Possibly they were involved in collecting food that had been cut by the shearing crests, so that it could be picked up by the tongue.

The origin of the tribosphenic molar has been discussed in functional terms by Mills (1964, 1967), Crompton (1971), Butler (1972) and Bown & Kraus (1979), among others. *Kuehneotherium*, *Amphitherium*, *Peramus* and *Aegialodon* are believed to represent successive stages of advance, though they do not form a phyletic series. Upper molars are known only in *Kuehneotherium* and *Peramus*, and the mode of origin of the protocone remains speculative. The principal changes involved were probably as follows (Fig. 8).

Starting from a form with occlusal relations like *Megazostrodon*, the cutting edge was folded by shifting upper cusp B buccally and lower cusp c lingually. Shear between the upper A-B crest (paracrista) and the lower a-c crest (protocristid) thus became more transverse, as in *Kuehneotherium*. The next step was the development of a talonid behind the metaconid (c), down which the paracone (A) travelled as the paracrista sheared against the protocristid, as in *Amphitherium*. Primitively the paraconid (b) extended forward to occlude between the paracone (A) and metacone (C) of the more anterior upper molar. This relationship had been lost in *Peramus*, where the paraconid occluded posteriorly to the metacone, and a rudimentary hypoconid, developed on the talonid crest, sheared in the paracone-metacone notch. A possible intermediate stage is seen in *Amphitherium* (Fig. 8A). Here the talonid, smaller than in *Peramus*, is overhung by the paraconid of the following tooth, and facets on the paraconid, due to wear against the paracone and metacone, are continued down onto the lateral surface of the talonid. As the talonid lengthened and the paraconid retreated, it is possible to imagine these facets being transferred from the paraconid to the talonid.

In *Shuotherium* (Chow & Rich, 1982), from the Late Jurassic of China, the paraconid was

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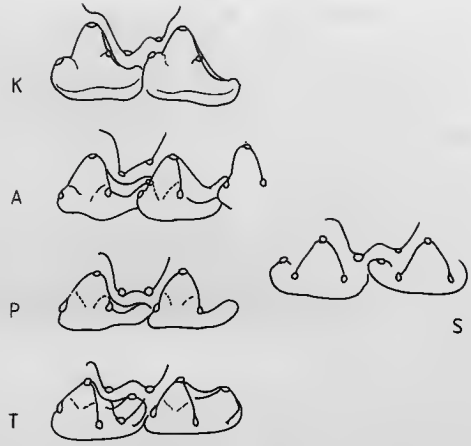

FIG. 8. — Stages in the evolution of tribosphenic molars.
K, *Kuehneotherium*; A, *Amphitherium*; P, *Peramus*; T, tribosphenic. The teeth are drawn as seen in the direction of the closing movement. Note the retreat of the paraconid as the talonid develops, so that the hypoconid eventually replaces the paraconid in the paracone-metacone notch. The protocone develops only in the final stage. In *Shuotherium* (S) a pseudotalonid develops anterior to the trigonid.

displaced from the paracone-metacone notch, not by the hypoconid but by a cusp that developed on a pseudo-talonid at the anterior end of the lower molar. This cusp is not present on M_1, where presumably the paraconid occluded between the paracone and metacone of P^4. The lower premolars have well developed paraconids, unusual in Mesozoic mammals.

The protocone appears to have arisen as an elevation of the cingulum, lingual to the paracone. It would thus have come up against the talonid crest on the lingual surface of the small hypoconid, providing a crushing area. Increase of the area of contact would be achieved by widening of the talonid, the hypoconid shifting buccally. The enlarging protocone would develop an occlusal relation with the posterior surface of the metaconid, and with the formation of a preprotocrista, the protocone would supplement the paracone in shearing with the protocristid. The talonid crest, which originally connected with the tip of the metaconid, would join the posterior wall of the trigonid in a more buccal position (Fox, 1975; Butler, 1978). The entoconid-postprotocrista shear probably developed later, as it is absent in some Cretaceous mammals (*Kermackia, Kielantherium*). Opposition between the paracristid and the hypocone cingulum arose still later; the earliest example is *Kennalestes* (Crompton & Kielan-Jaworowska, 1978).

If their evolution has been correctly reconstructed, docodonts and therian mammals both developed a cusp on the upper cingulum, lingual to the paracone, which opposed the top of a crest near the posterior end of the corresponding lower molar (Fig. 9). The area of opposition

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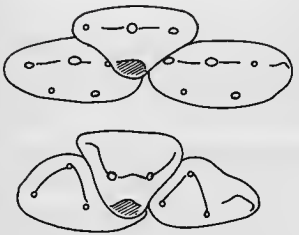

FIG. 9. — Hypothetical initial stages of crushing contact in an ancestral docodont (above) and an ancestral tribosphenic mammal (below).

formed a crushing surface that operated at the end of the upward masticatory stroke, i.e. in centric occlusion. This surface became extended transversally, and an additional area of opposition developed against the anterior part of the more posterior lower molar. Lingual-phase facets were produced by sliding contacts between the crushing areas during the early stage of jaw-opening.

This parallelism was superimposed on a preceding divergence which took place when the molars had only a shearing function. Both groups were probably derived from a form with triconodont molars having occlusal relations like those of *Megazostrodon*. Therian molars developed a capacity for transverse shearing, and the differentiation of the talonid was probably an aspect of this; docodonts retained the primitive longitudinal shear, perhaps due to a restriction on transverse jaw movement.

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During visits to the United States in 1965-6 and 1974 I was able to examine specimens in several museums, and I wish to thank particularly Dr Craig C. Black (Carnegie Museum), Dr C. Lewis Gazin (U.S. National Museum) and Dr P. D. Gingerich (Yale Peabody Museum) for their generous help. Thanks are also due to Dr K. A. Joysey (University Museum of Zoology, Cambridge) and Professor R. J. G. Savage (Bristol University). Dr G. Krusat (Freie Universität Berlin) kindly allowed me to examine the *Haldanodon* material on which he was working. I am also grateful to Dr P. D. Gingerich for stimulating discussion and for casts of specimens. At the British Museum (Natural History) Dr J. J. Hooker provided much appreciated practical assistance, and Dr D. Claugher took scanning electron micrographs.

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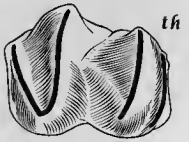
DIET AND TOOTH WEAR



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Molar Morphology and Tooth Wear

J. R. E. MILLS

ABSTRACT

In those reptiles which lay on the line leading to the evolution of mammals, chewing was impossible. The teeth served only to seize the prey. With the development of the dentary-squamosal joint, lateral jaw movement evolved. The teeth could therefore be used as a cutting mechanism, to divide the prey into ingestible pieces, necessary in a warm-blooded animal with a higher metabolic rate. The wear on the molar teeth formed a self-sharpening device.

The talonid originated as a protection for the point of contact of the teeth, but in many genera, including most primates, developed into a basin into which the protocone occluded. Chewing took place in two phases: a buccal phase, from first contact to the centric position, with horizontal rotation about the ipsilateral condyle, passing into a lingual phase, with rotation about the contralateral condyle, each cusp and crest having a precise function against a corresponding structure in the opposing tooth. In many species, including *Gorilla* and man, the cusps, especially those involved in the lingual phase, wear rapidly to expose the dentine, and this alternation of hard enamel and softer dentine forms an efficient grating and shredding apparatus, as in herbivorous mammals. The lingual phase and consequent " balancing occlusion " are thus eliminated.

RÉSUMÉ

Chez les reptiles qui sont dans la filiation des Mammifères, la mastication était impossible. Les dents ne servaient qu'á saisir les proies. Avec le développement d'une articulation dentaire-squamosal, le mouvement latéral des mâchoires est intervenu. Les dents ont pu alors être utilisées comme un mécanisme coupant, pour diviser la proie en fragments susceptibles d'être ingérés, ce qui est nécessaire á un animal á sang chaud et à métabolisme élevé. L'usure des molaires entretenait une affûtage permanent.

Le talonide constituait á l'origine une protection pour le point de contact des dents, mais dans de nombreux genres, y compris la plupart des Primates, il a évolué en un bassin avec lequel le protocone entre en occlusion. La mastication a comporté deux phases : une phase buccale, depuis le premier contact jusqu'à une position centrale, avec rotation horizontale autour du condyle ipsilatéral, passant ensuite à une phase linguale avec rotation autour du condyle contralatéral, chaque tubercule et crête ayant une fonction précise par rapport à une structure correspondante de la dent opposée. Dans de nombreuses espéces, incluant le gorille et l'homme, les tubercules, surtout ceux qui sont impliqués dans la phase linguale, s'usent rapidement jusqu'à la dentine, et de cette alternance d'émail dur et de dentine plus molle résulte un appareil qui rape et déchire de façon efficace, comme chez les mammifères herbivores. La phase linguale et l' «occlusion équilibrante » qui en résulte sont ainsi éliminées.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 343-350.

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Source : MNHN, Paris

Reptiles, at least that line which leads to the mammals, have upper and lower teeth which do not occlude. The lower teeth close entirely within the upper teeth, and serve merely to seize the prey and to some extent pound it, but without any chewing action. The jaw joint between the quadrate and articular bones does not allow any lateral jaw movement. In the earliest known mammals a number of changes have taken place. They were probably to some extent warm-blooded. Being very small, they would require a large intake of food relative to their size. An ability to cut up food into ingestible pieces would be an advantage, and this became possible due to the development of a new jaw joint between the dentary and squamosal, with corresponding changes in the musculature. Thus in *Kuehneotherium*, the earliest known therian mammal, the seizing and piercing activity was probably still predominant, but the animal was now capable of moving its mandible forwards and medially, thus pressing lower molars against the uppers, introducing a cutting action between the sharp edges of the crests running mesially and distally from the tips of the principal cusps. In addition to this lateral movement, there was probably some rolling action at the mobile symphysis as is seen in *Tenrec* (Mills, 1966) and in *Didelphis* (Hiiemae & Crompton, 1971). When viewed from above, the teeth of *Kuehneotherium* appear triangular, with the buccal apex of the lower molar fitting between two upper molars, and the lingual apex of the upper similarly between two lower teeth. This shearing action between teeth was so successful that it became the basis for the mammalian molar dentition in general, and may still be seen in recent mammals such as the zalambdodont insectivores. However, if the principal cusp of one tooth were to shear exactly on the point of contact of its two opponents, it would have the effect of impacting the food between the opponents. This feature is well known to dentists in the human dentition, where in filling a posterior tooth, its margin is built up as a " marginal ridge " to protect the contact point. This is produced in *Kuehneotherium*, by the hook-shaped stylocone and parastyle on the upper tooth and the incipient talonid on the lower.

As the lower teeth are pressed against the uppers, the sides of the cutting crests are worn, with the appearance of facets. This wear of the enamel is parallel to the tooth surface, and has the effect of maintaining the sharp cutting edges, in a manner analogous to the sharpening of a chisel. Every (Every & Kühne, 1971) has called this action " thegosis " and suggests that it does not occur primarily in mastication, but is a deliberate " gnashing of the teeth " at times of stress, in order to maintain the sharpness of the teeth.

This mechanism of reversed triangles, with sharp cutting edges, was (and in the zalambdodont insectivores still is) a very efficient mechanism for cutting up the the hard chitin of insects and perhaps small crustaceans. The point of contact of the lower molars was protected by the incipient talonid, which gradually came to lie on the buccal side of the paraconid of the lower molar, and increased in size. It thus formed a second, auxiliary cutting edge, with the upper tooth developing additional cusps in the centre of its crown, between which the newly-developed hypoconid of the lower molar could shear, virtually doubling the cutting edge of the tooth without appreciably increasing its length. The wear in chewing or in " thegosis " maintained a sharp edge. This may be visualised in *Pappotherium* from the early Cretaceous. Fig. 1 is a simulation of the chewing action in this animal, the lower molars being based on those described by Patterson (1956). The same self-sharpening mechanism is seen in all those mammals, usually carnivores, where chewing is essentially confined to a cutting action. It is seen in an extreme form in the cat family.

By the time the earliest primates had evolved, in the latest Cretaceous, the original system of reversed triangles was still recognizable, but an important development had occurred. The small, hook-shaped talonid of *Kuehneotherium* had developed into a basin, into which the protocone of the upper molar fitted in the centric position. This is illustrated in Fig. 2, in the case of the recent tree-shrew *Tupaia*, although a similar situation would be present in the earliest primates, such as *Purgatorius*. Osborn (1888) described this as a pestle-and-mortar relationship, but this is not an exact analogy A pestle works in a mortar either by a pounding action or by a multidirectional grinding action. In the early Primates, and in modern lemurs and tarsiers the protocone sweeps across the talonid basin along a single path with a shearing action between the sides of the various

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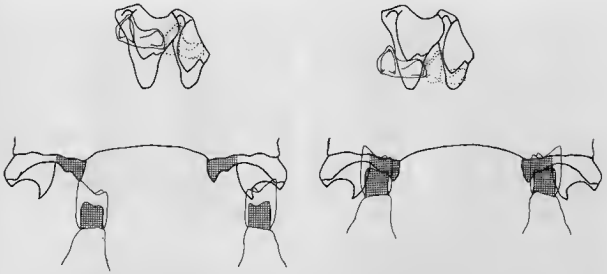

FIG. 1. — Diagrammatic reconstruction of chewing in an early mammal such as *Pappotherium*. Above occlusal view; Below in cross-section through the centre of the talonid, on the left at the first contact of upper and lower teeth, on the right at the end of chewing stroke.

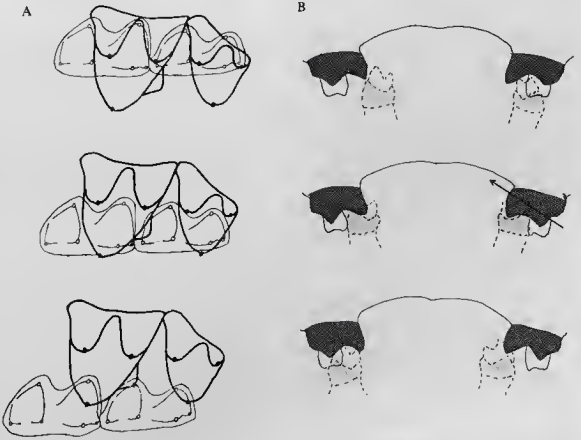

FIG. 2. — Diagrammatic reconstruction of chewing of a primitive primate, here represented by *Tupaia*. A, occlusal view; B, cross-section through the talonid. In both cases uppermost diagram at beginning of buccal phase, centre diagram in centric jaw relation, lowest diagram, the lingual phase.

Source : MNHN, Paris

crests which connect the cusps. This involves a more horizontal jaw movement and requires two changes. In the first place, the jaw movement is more horizontal, as shown by the arrow in the centre diagram of Fig. 2B, but the sides of the crests are still kept in contact, to maintain the sharpening activity. The cusps therefore rotate so that their occluding faces come to lie rather more horizontally, parallel to the direction of jaw movement and the external row of " styles " on the upper molars is gradually reduced both in height and in bucco-lingual width. Secondly, the amount of movement of the lower jaw is considerably greater than in the early carnivores, where the teeth are merely pressed together. If the lateral movement were still provided by a simple antero-medial translation of the head of the mandibular condyle in the glenoid fossa of the squamosal, the latter would become impossibly wide. This is overcome by a system whereby the mandibular condyle rotates in the horizontal plane, in addition to some translatory movement.

In a chewing cycle, therefore, the lower posterior teeth move upwards and medially until they meet their antagonists. Each lower buccal cusp shears between two upper cusps, with their mesially and distally directed crests producing a rather blunt cutting action, as illustrated in the top diagram in Fig. 2B. The distal side of the lower trigonid shears inwards, pressed closely against the mesial side of the upper tooth, with an ideal cutting action. The protocone of the upper molar moves buccally down between the metaconid and ento-conid of the lower molar into the centre of the talonid basin, as shown in the centre diagram of Fig. 2B, again with a rather blunt cutting, or grinding action. This completes the buccal phase of occlusion, but as the primates develop so does a lingual phase of occlusion, with the lower tooth continuing to move inwards, although with an anterior component, as rotation is now about the opposite mandibular condyle. The buccal face of the upper molar shears, surface-to-surface, across the lingual face of the hypoconid of the corresponding lower molar, as in the bottom diagram of Fig. 2B. In the more primitive primates the lingual end of the trigonid of the lower molar continues in contact with the mesio-lingual side of the upper protocone.

From here the step to the Hominoidea is a fairly simple one, with the elimination of the already decreased system of reversed triangles. The raised trigonid of the lower molar is reduced to the level of the talonid, with the elimination of the paraconid, whose function is largely taken over by the entoconid, on the disto-lingual margin of the more anterior lower molar. At the same time the triangular outline of the upper molar becomes quadrangular, with the development of the disto-lingual hypocone of the upper tooth. This last cusp sweeps across the original trigonid basin of the lower tooth, duplicating the action of the protocone across the talonid. This can be seen in apes such as *Proconsul* or the recent Gorilla, as shown in Figs. 3 and 4, and indeed in man.

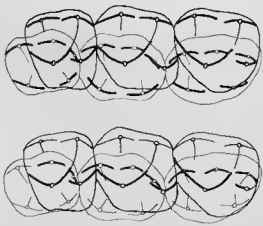

FIG. 3. — Upper and lower molars of *Gorilla* superimposed in centric position. The heavy lines in the upper diagram indicate those crests involved in the buccal phase of occlusion, while in the lower, the heavy lines are those crests in the lingual phase.

The unworn teeth in these species show a very elaborate mechanism. In the buccal phase the protocone of the upper tooth shears down between the metaconid and entoconid of the lower tooth as the mandible rotates about the ipsilateral condyle, and then, moving into the lingual phase, it changes direction as the mandible rotates about the contralateral condyle, and its flat, almost horizontal, buccal face slides across the upper face of the hypoconid. The hypocone similarly shears initially between the metaconid of a lower molar and the entoconid of the tooth anterior to it, then, in the lingual phase, its buccal face slides across the lingual, upper face of the protoconid of the more

Source : MNHN, Paris

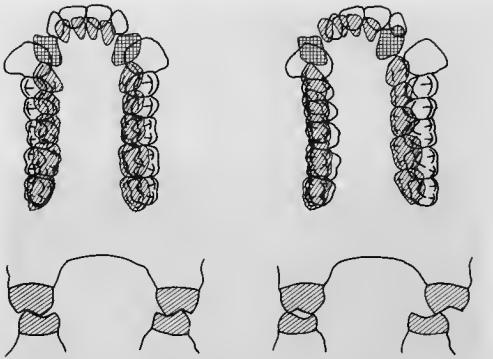

FIG. 4. — Upper and lower teeth of *Gorilla* superimposed on the left in the centric position, on the right showing buccal phase on the left side simultaneously with the lingual phase on the right side. Upper occlusal and lower cross-section of molars.

posterior tooth. It will be noted from Fig. 4 that the buccal phase on one side of the mouth coincides with a reversed lingual phase on the other, and vice versa, producing a so-called balanced occlusion. A close examination of slightly worn molars will show that each minor cuspule and ridge on the tooth has a function in association with an opposing tooth. The cusps of the lower molars, similarly and reciprocally, shear across the upper teeth, as shown for *Gorilla* and man in Fig. 5. It will be noted that the jaw movement changes direction as the cusps move from the buccal to the lingual phase.

I described the above action as it concerns primates in a paper which I wrote in 1955, deducing the direction of jaw movements from wear facets on the teeth. I encountered some difficulty because, in order to identify the facets, it was necessary to select skulls in which the wear had not penetrated through the enamel to the dentine. This occurs at a rather early stage, leaving a shallow depression in the dentine, surrounded by a rim of enamel. In many cases in the gorilla the first molar was quite worn on the upper lingual and lower buccal cusps (the cusps involved in the lingual phase of occlusion) before

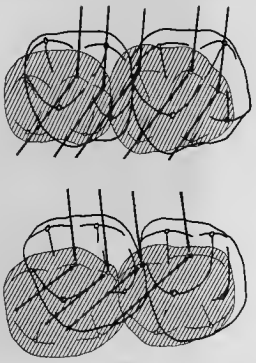

FIG. 5. — Upper and lower molars of, upper diagram *Gorilla*, and lower diagram Man, superimposed in centric relation. The straight lines show the paths of the lower buccal cusps across the upper teeth.

Source : MNHN, Paris

any appreciable wear of the enamel of the third molar. The same type of wear is found in the human molar dentition, as illustrated in the Saxon skull from the Odontological Museum of the Royal College of Surgeons in London, illustrated in Figs. 6 and 7. It will be seen in Fig. 6 that, although the buccal side of the lower and lingual side of the upper first molars, are extensively worn, and those of the second molars moderately so, the third molars show only slight wear. The individual was presumably a young adult, probably under twenty years of age. Turning to Fig. 7A, the occlusion of this skull is seen in the buccal phase of occlusion, with the worn teeth in contact over their entire surfaces. In Fig. 7B is illustrated the vestigial lingual phase, now confined to the third molars, and this also would doubtless soon have worn away had the individual lived a few more years.

FIG. 6. — A, upper and B, lower molar teeth of the Saxon skull. Note extensive wear on first molar, although the third molar is almost unworn.

Source : MNHN, Paris

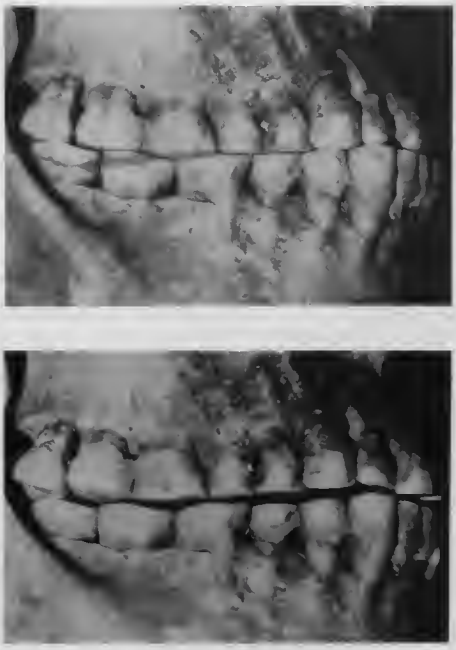

FIG. 7. — Simulated chewing in the same Saxon skull as Fig. 7. A, in the buccal phase. B, in the vestigial lingual phase. Contact is confined to the third molar.

Molar wear in mammals takes essentially two forms, with minor variations. In carnivorous species, including many insectivores, the enamel is fairly thick, and wear is parallel to the lingual surface of the upper and buccal surface of the lower teeth. This produces a self-sharpening mechanism to maintain the essentially cutting action required. In herbivores and many rodents and lagomorphs the teeth are covered with enamel when they erupt, but this wears rapidly, leaving the dentine exposed. This forms an efficient grinding mechanism, since the dentine wears rapidly, leaving a sharp rim of enamel around its periphery. This shreds the food

Source : MNHN, Paris

efficiently similarly to a grater used in the kitchen for the same purpose. In many herbivorous mammals this is confined to the buccal phase of occlusion, while in lagomorphs and some rodents it occurs in the lingual phase. This would seem to be the situation in many of the primates. It is most extreme in the cercopithecoid monkeys, where the lingual phase is transient and rapidly disappears as the upper lingual and lower buccal cusps are worn down, leaving only the buccal phase.

The same thing happens rather more slowly in the great apes and man, so that in a mature individual chewing is confined to the buccal phase. In order to maintain this grating action, two substances of differing hardness, wearing at different rates, are necessary. If only enamel were present on a worn tooth, the polished surface would be as useless as a glazed grindstone.

If, as seems to be the case, this is the most efficient way to use the hominoid molar teeth, it is difficult to see why the shape of the unworn teeth, with its intricate pattern of cusps and fossae, ridges and grooves, has evolved.

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Source : MNHN, Paris

The Transition from Insectivory to Herbivory in Mammalian Teeth

J. M. RENSBERGER

ABSTRACT

The transition in therian mammals from insectivory to ungulate herbivory that began near the Cretaceous-Tertiary boundary was accompanied by pronounced changes in molar structure. Included in these changes were several basic aspects that determine occlusal pressure, amount of increased surface area produced per chewing stroke, and length of shearing movement of opposing surfaces. Measurements of these attributes in representatives of extant and fossil insectivorous and herbivorous mammals point to a change in the way food was broken down. The chewing system in the insectivores combines shearing, resulting from high angle translative movement, with compressive food breakdown, but was dominated by shearing. The chewing system in the early ungulates was dominated by compressive action. Therefore, the more or less horizontal shearing mode in many later Tertiary herbivores resulted from the re-establishment of new shearing mechanisms. These results are consistent with other data based on microwear and directional trends of enamel structures.

RÉSUMÉ

Le passage, chez les Mammifères thériens, du régime insectivore au régime herbivore, qui débuta au voisinage de la limite Crétacé-Tertiaire, s'accompagna de changements prononcés dans la structure des molaires. Parmi ces changements se trouvent plusieurs aspects fondamentaux qui déterminent la pression d'occlusion, l'amplitude d'accroissement de la surface produite par les mouvements de mastication, et la longueur du mouvement tranchant des surfaces antagonistes. La mesure de ces facteurs chez des représentants des mammifères insectivores et herbivores fossiles et actuels indique qu'un changement est intervenu dans la façon dont la nourriture était désagrégée. La mastication des insectivores combine l'action tranchante, résultant d'un mouvement de translation à angle élevé, avec la désagrégation de la nourriture par compression, mais l'action tranchante est dominante. Chez les premiers Ongulés, l'action de compression constituait l'élément dominant du système masticateur. Par conséquent le type tranchant plus ou moins horizontal de nombreux herbivores du Tertiaire plus tardif fut la conséquence du rétablissement de nouveaux mécanismes tranchants. Ces résultats concordent avec d'autres données basées sur la micro-usure et sur les tendances évolutives des structures adamantines.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 351-365.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

The mechanics of many of the mobile skeletal structures of vertebrates are moderately well known. The cheek teeth in mammals are an exception. The functional dynamics of the mammalian teeth have interested workers at least since the later part of the nineteenth century when workers began to observe differences in mechanical behavior, especially direction of movement of the jaws and teeth (Hunter, 1861; Ryder, 1878; Cope, 1889). Nevertheless, we are still not able to explain the differences in structure of the multicusped tooth crowns in most Cenozoic mammals. These complex morphologic structures are not largely random, judging from the similarities of patterns acquired independently by members of different phylogenetic lineages. One of the difficulties of interpreting the functions of the differing mammalian cheek tooth structures is that the events of importance occur in a brief moment as the rapidly moving jaws come together. The 3-dimensional relationships of the structures and the complexity of the events occurring when opposing teeth collide make the problem difficult to study. Furthermore, there are probably multiple pathways that provide more or less equivalent solutions to adaptative problems. Although certain aspects of the occlusal relationships and function in some groups have been studied (Butler, 1952, 1972, 1973; Mills, 1955; Crompton, 1971; Kay & Hiiemae, 1974; Rensberger, 1975; Janis, 1979), functional explanations for morphologic structures have not been found for most groups.

One of the most conspicuous events in the evolution of the mammalian cheek teeth was the transition from insectivory to herbivory at the end of the Cretaceous and into the early Tertiary. Studies have been made of occlusal relationships in taxa on both sides of this boundary, but relatively little attention has been given to the transition itself. Rensberger (1986) presented data suggesting an increasing dominance of compressive chewing action in several major groups of early Tertiary ungulates. The present paper provides data on other quantitative changes in functional characters across this adaptative transition.

Functional characters.

The functional efficiency of the cheek teeth in mammals can be defined as the increase in food surface area produced per occlusal stroke. This quantity is controlled by several basic factors:

— Area of dental structures effective in exerting strain on foods parts.
— Resistance of food to fracturing.
— Occlusal pressure exerted on the food.
— Effects of pressure and abrasion on dental structures (i.e., changes in the food processing efficiency of the tooth with wear).

Characters in advanced herbivores.

The functional aspects of cheek teeth in certain later Cenozoic herbivores can be recognized because of the pronounced specialization of the structures and the relative simplicity of the endpoint form. In taxa in which chewing movement is parallel to the occlusal surface, effective dental area is equivalent to the lengths of the contacting edges measured in a plane perpendicular to the direction of movement. This can be visualized intuitively because it is the upstroke corner of an enamel facet, not the occlusal face of the facet, that grips the food fibers and causes the shearing. Thus, in herbivores with high cheek tooth crowns and flat occlusal surfaces, the directions of the enamel edges tend to be aligned parallel to one another and perpendicular to the direction of chewing (Fig. 1A), an alignment that maximizes the interception of food that is dragged along by the movement of the opposing surface. In these mammals the chewing direction is strongly translational, that is, the opposing teeth slide parallel to one another. Enamel is often infolded to form multiple parallel cutting blades (Fig. 1A). Parallel edges are one mechanism that maximizes "effective area" in translational systems. Widening of the tooth perpendicular to the chewing direction to allow longer edges is another, perhaps simpler, structural change that would maximize effective area, but this pathway seems to be seldom taken, probably because there are limits to tooth width owing to other constraints.

Enamel tends to become relatively thin in translational systems that are highly lophodont. This reduces the actual surface-to-surface contact

Source : MNHN, Paris

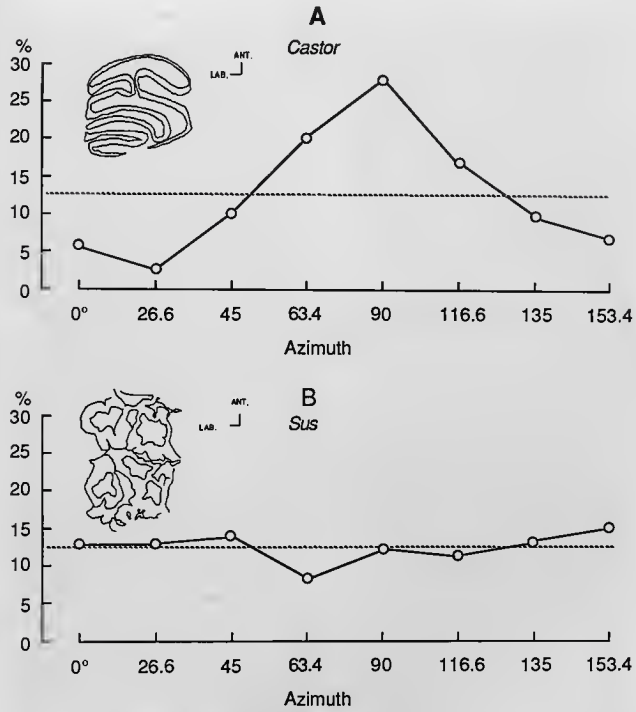

FIG. 1. — Percentage frequencies of enamel edge directions in right upper molars with (A) strongly directional pattern and (B) strongly random pattern (A, beaver; B, pig). Dashed line represents level of hypothetical random distribution. Totals of 1809 and 1578 directions per tooth were measured in *Castor* and *Sus*, respectively. 0° = anteroposterior, 90° = transverse. Anteroposterior here represents direction parallel to long axis of tooth row, not parallel to midline of palate. Fractional values of azimuth classes and slightly varying class widths result from extracting directions from digital images by calculating direction of three successive pixels (picture elements) along an edge (Rensberger, Forsten & Fortelius, 1984). Chewing orbit in *Cavia*, a rodent with strongly directional edge pattern as in *Castor*, with horizontal component 75 % of vertical component (calculated from unilateral cycle in Byrd, 1981). Horizontal component of chewing orbit in *Sus* 27 % of the vertical component (from cycle 1 in Herring & Scapino, 1973). Chewing direction in horizontal plane in A close to 0°, based on consistent striae directions. Striae directions variable in *Sus*.

Source : MNHN, Paris

area between opposing teeth (area in the horizontal plane) and therefore increases occlusal pressure (factor 3). A simulation of translating surfaces modelled after actual occlusal patterns has shown that the pressure is raised still further by the tendency for only a few edge areas to be in opposition at any given moment during the occlusal stroke (Rensberger, 1973). A consequence of the high occlusal pressures generated in this type of mechanism and the abrasive nature of the tough materials requiring the high pressure, is a high rate of wear (factor 4), hence the association of at least some degree of hypsodonty in these teeth. The hypsodont teeth tend to have parallel sides so that the tooth and its shape are maintained in the presence of high rates of wear.

However, some later Cenozoic herbivores, such as pigs, peccaries, and the extinct entelodonts, lack such structural tendencies. In these forms the enamel shell of the cusps tends to be cylindrical and to form nonaligned edges when breached by wear. The lack of a preferential direction in the enamel edges indicates a dominance of compressive as opposed to translative action between opposing surfaces. Here the amount of food processed is again dependent upon the "effective area" but, because the direction of motion is predominantly perpendicular to the occlusal surface, the effective area is measured in the occlusal plane and efficiency is proportionate to the occlusal area. Selection favors simply large areas, and often there is little or no preferential direction to the edges of enamel. With the aid of a computer algorithm one can measure the edge directionality in a tooth (Rensberger, Forsten & Fortelius, 1984). Figure 1 compares the directionality of the enamel edges in a highly specialized translational dentition and in a specialized compressional dentition. In the former the mandibular dentition moves parallel to the anterior axis of the tooth, and the directional emphasis of the edges centers at 90° from anterior. In the compressional tooth the direction of motion is more nearly vertical, with no preferred direction in the horizontal plane, and the directions of the edges are essentially random (frequencies form a nearly flat curve, close to 12.5 %).

Attainment of high occlusal pressures in compressive type systems is limited because selection tends to produce large occlusal contact areas. For flexible foods which broadly contact the occlusal surface, this type of dental mechanism is limited to materials that can be fractured by relatively low occlusal pressures. This mechanism is efficient, for example, in chewing fruits, which fracture easily, but not grasses. However, it is effective for seeds with relatively inflexible shells that concentrate stress in a small part of the occlusal surface and are fractured by high pressures (Lucas, 1979: 494).

The functional differences in the occlusal morphology in the two examples of Fig. 1 are closely related to differences in chewing motion and occlusal pressure. These are basic factors that must be known if the occlusal function is to be fully understood. Chewing directions can be inferred from striae on the chewing surfaces. Occlusal pressures are determined by the relationship between the masticatory force vector and the attitudes of surfaces, and the latter, at least, may be observed on the teeth. Hylander (1985) has been able to measure stress in the mandible in living animals using strain gages, and this offers a potential for measuring the magnitudes of the masticatory force acting on the cheek teeth.

Characters in primitive mammals.

The dental structures of the Cretaceous insectivores and early ungulates are more difficult to analyze functionally than are the teeth of the highly specialized herbivores. The relationships are more complex because contact between opposing cheek teeth occur in multiple, nonparallel planes on surfaces of very high relief. Some of the functionally important data about insectivore-grade teeth is available, however. Jaw movements, and homologies of occlusal contact areas, and in some cases changes in size of contact areas have been described by Butler (1952), Mills (1955, 1966), Crompton & Hiiemae (1970), Crompton (1971), Crompton & Kielan-Jaworowska (1978), and other studies cited in Hiiemae (1978).

Butler (1972) provided data on the chewing direction in Cretaceous taxa. He traced one quantitative character, the change in chewing direction in the transverse vertical plane, in a series of Mesozoic taxa ending with *Protungulatum*, the earliest known ungulate. The chewing direction in the transverse plane changed from

Source : MNHN, Paris

about 35° (angle measured from vertical to horizontal) in the Rhaetic (late Triassic) *Kuehneotherium* to about 55° in *Protungulatum* in the late Cretaceous. Butler noted that this trend toward a less vertical angle continued into Tertiary herbivores, but did not document the trend beyond the late Cretaceous. Rensberger (1986) measured the chewing direction in the vertical transverse plane in the late Cretaceous palaeoryctid insectivore *Procerberus*, in *Protungulatum*, and in several groups of Paleocene and Eocene condylarths.

The chewing angles in Butler (1972) are based on striae occurring high on the posterior face of the trigonid and the opposing surface on the anterior side of the upper molar. Because of the high angle of these surfaces in the insectivores, the direction of the striae in each case probably closely approximates the force vector of the masticatory muscles in the transverse plane, that is, there has been relatively little deflecting effect of the contacting surfaces on the mandibular movement.

Because occlusal pressure depends upon both the direction of the masticatory force and the attitude of the surface upon which the force acts, changing surface attitudes are important functional characteristics in a system undergoing adaptive modification for new food types. An additional factor that is measurable in primitive mammals is the length of the chewing stroke, which determines in part the amount of increased food surface area produced per stroke. In the flat occlusal surfaces of the hypsodont herbivores with horizontal translation, the length of the occlusal stroke is not limited or defined by dental structures and is difficult to measure in extinct taxa. In the insectivores, however, the length of the occlusal stroke is measurable as the distance from the highest cusp of the trigonid to the talonid basin. The level of the center of the talonid basin is the greatest depth to which the occluding protocone may descend.

Material and Method

Six characteristics were measured in the upper or lower first or second molars of insectivorous and herbivorous taxa. The characters include occlusal surface attitudes, the length of the occlusal stroke, and a measure of the size of the tooth. Size was a changing factor itself in the transition from insectivory to herbivory and is also needed to facilitate comparison of stroke length among taxa of different sizes.

Surface attitudes.

The surface attitudes were measured as angles between adjacent surfaces or between a surface and the vertical direction. Ideally one would measure all angles with respect to a reference direction, but with fossils consisting of isolated teeth this is often difficult in practice. Root and crown development varies between taxa so that the vertical axis of a tooth is often difficult to determine. After examining teeth in numerous taxa I found that the angles between adjacent surfaces of the major cusps could be measured with more consistent results.

One of the surfaces, the posterior shearing surface on the trigonid, has no adjacent surface that serves as a convenient reference. The attitude of this surface was measured from vertical, with the tooth being held so that the root under the trigonid is vertical.

Surface angles measured (see also Fig. 2):

Upper Molar

PaT/ = angle defining taper of paracone in labial view.

Pa-MeN/ = angle of notch between paracone and metacone in labial view.

Lower Molar

/TrPA = angle between posterior trigonid surface and vertical axis of trigonid.

/Tr-TaD = trigonid-talonid displacement (difference in height between the top of the trigonid and talonid basin).

Size measurements:

Upper Molar

WT/ = transverse width of tooth (greatest transverse dimension).

Lower Molar

/WTr = transverse width of trigonid.

Dentitions in moderate stages of wear were selected, so that the data reflects typical occlusal morphology in mature but not old individuals. The measurements were taken on representatives of the following taxa.

Source : MNHN, Paris

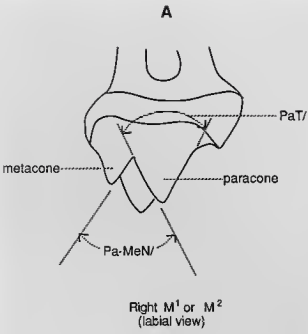

FIG. 2. — Measurements of functional characters taken in upper and lower molars. A, upper molar and B, lower molar of *Procerberus*. Abbreviations in this and later figures: PaT/ = angle in anteroposterior plane of taper of paracone; Pa-MeN/ = angle in anteroposterior plane of notch between paracone and metacone; /TrPA = angle in anteroposterior plane between posterior wall of trigonid and vertical line; Tr-TaD = depth of talonid basin beneath top of trigonid.

A. *Insectivores*

MARSUPIALIA

Didelphidae
Metachirops (Recent)
Caluromys (Recent)

EUTHERIA

Palaeoryctidae
Procerberus (late Cretaceous)

Zalambdalestidae
Zalambdalestes (late Cretaceous)

Deltatheridiidae
Deltatheridium (late Cretaceous)

Erinaceidae
Erinaceus (hedgehog, Recent)

Talpidae
Scapanus (mole, Recent)

Soricidae
Sorex (shrew, Recent)

Vespertilionidae
Myotis (brown bat, Recent)

B. *Herbivores*

EUTHERIA

Arctocyonidae
Protungulatum (late Cretaceous)
Eoconodon (early Paleocene)
arctocyonid (early Paleocene)

Phenacodontidae
Tetraclaenodon (middle Paleocene)
Phenacodus (early Eocene)
Ectocion (early Eocene)

Equidae
Hyracotherium (early Eocene)

Isectolophidae
Homogalax (early Eocene)

Hyrachyidae
Hyrachyus (early Eocene)

Brontotheriidae
Lambdotherium (early Eocene)
brontotheriid (late middle Eocene)
brontotheriid (late Eocene)
Brontotherium (early Oligocene)

Source : MNHN, Paris

The partitioning of the fossil taxa of this list into insectivores and herbivores is based on feeding habits of living descendants of lineages and similarity of the teeth to those of living taxa. The dentitions of the extinct taxa assigned to the insectivores are similar in overall morphology to those of living insectivores. All of the living descendants of the arctocyonids but the Cetacea are herbivores. Some of the early ungulates may have been omnivorous, but in the discussion below the dietary groups will be called insectivores and herbivores. There may be errors in some of these assignments. For example, *Protungulatum* may in reality have been a large insectivore. By quantifying characters of fundamental functional importance to the masticatory system, we can assess the degree of functional resemblance between taxa and the consistency of the dental form with the dietary hypotheses. With these data, the functional proximity of uncertain taxa to taxa of known diets become more apparent. The morphology that has been used to classify the fossils phyletically is also largely dental, but is much broader, not being subject to the functional choices made here.

Results

Angular measurements.

Of the two angular measurements taken on the upper molar surfaces, the taper angle of the paracone is more consistent among members of a single taxon and more clearly separates the insectivores and herbivores. The other measurement, the angle of the notch between the paracone and the metacone, strongly correlates with the paracone taper. The paracone taper angle clusters the insectivores at the low end of the range of values (Fig. 3). The didelphid marsupials are the only insectivores that fall into the range of the herbivores. Among the ungulates, specimens representing the arctocyonids, the phenacodontid genus *Ectocion*, the early horse *Hyracotherium*, the primitive rhinocerotoid *Hyrachyus*, and the primitive brontothere *Lambdotherium* each cluster rather close to one another. There is a rough correlation (correlation coefficient = .49) between size, as indicated by the width of the molar, and the paracone taper angle (Fig. 3). However, when the large brontotheres are excluded

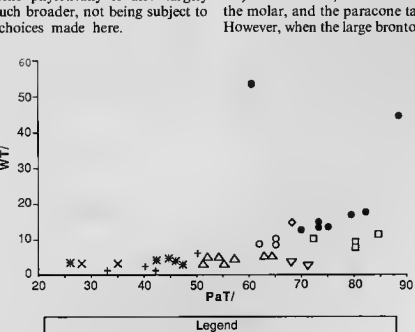

FIG. 3. — Scatter diagram of paracone taper angle (PaT/) versus width of upper molar (WT/) in insectivores and early herbivores. Width in millimeters, angle in degrees.

Source : MNHN, Paris

(Fig. 4), the correlation improves considerably (.78), suggesting that although the brontotheres were increasing in size in the Eocene, the taper angle was not increasing. When only the insectivorous taxa are considered (Fig. 5), the correlation is very poor (.18). Therefore, although the cusp taper angle increases with increased size, this change is mainly restricted to the insectivore-herbivore transition and within the primitive herbivores. The boundary angle that best separates the insectivores and herbivores is about 50°.

The paracone taper angle changes within the arctocyonid — phenacodontid — perissodactyl lineage (Fig. 6). Beyond the primitive perissodactyls (*Hyracotherium* and *Homogalax*), this increase stops at around 80° and may reverse itself in the case of *Hyrachyus*. *Hyrachyus*, other rhinocerotoids, and the tapiroids acquired a strong transverse lophodonty that is not present in the brontotheres or equids, and this secondary reduction of the taper angle may contribute to the maintenance of sharp-edged lophs in this group.

In the lower molar, the angle of the posterior shearing surface of the trigonid also correlates somewhat with size (correlation coefficient = .58) and, as in the case of paracone taper, the correlation is most evident in the transition between the insectivores and the herbivores (Fig. 7). However, the shearing angle further increased in the large brontotheres. The shearing angle in some of the herbivores overlaps that of the didelphids and the living hedgehog in the region between 19° and 25°. The group clustered at 0° in Fig. 7 consists of Cretaceous taxa (Fig. 8). Some increase in this angle may have occurred within lineages leading to the later Cenozoic insectivores.

The posterior trigonid shearing angle becomes abruptly larger in the transition from the Cretaceous insectivores to the earliest ungulates (Fig. 8). After that, the descendant phenacodontids and perissodactyls exhibit relatively little change. The large brontotheres have slightly larger shearing angles and *Hyrachyus* slightly smaller angles.

Depth of shear.

The depth of shear has a strong linear correlation with size, so that the large size increases in the transition from insectivore to herbivore and within the herbivores overwhelms this character. When the effects of size are reduced by taking the depth of shear as a percentage of the width of the trigonid, a separation of most of the insectivorous and herbivorous taxa is evident (Fig. 9). This character, among those measured, seems to separate the insectivores and herbivores the best. Only *Erinaceus* falls close to the herbivores in these

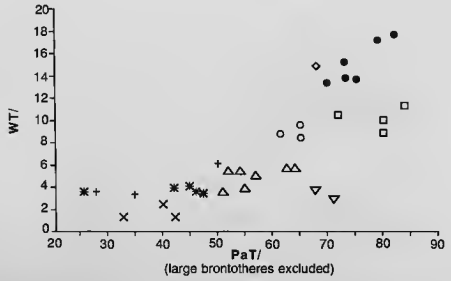

FIG. 4. — Scatter diagram of paracone taper angle (PaT/) versus width of upper molar (WT/) in insectivores and early herbivores, excluding late Eocene and early Oligocene brontotheres. Correlations coefficient = .78. For meanings of symbols, see legend of Fig. 3.

Source : MNHN, Paris

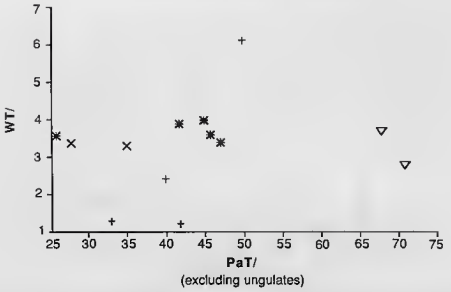

FIG. 5. — Scatter diagram of paracone taper angle (PaT/) versus width of upper molar (WT/) in insectivores alone. Correlation coefficient = .18. For meanings of symbols, see legend of Fig. 3.

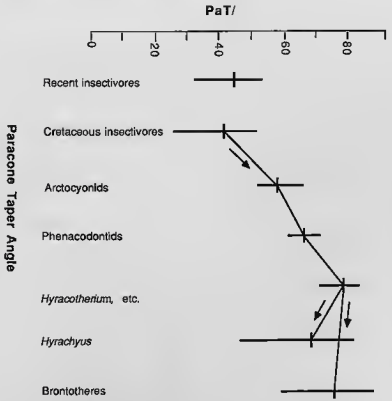

FIG. 6. — Differences in paracone taper angle among different groups of ungulates, compared to Cretaceous and Recent insectivores. Vertical lines are ranges, horizontal bars means. Lines joining means trace phyletic lines leading into perissodactyls. Cretaceous insectivores are mostly teeth of *Procerberus* and arctocyonids (mainly *Protungulatum*); dental structures of *Procerberus* are morphologically close to expected ancestral condition for *Protungulatum* (Sloan & Van Valen, 1965; Szalay, 1969); *Protungulatum* appears to be close to ancestry of later ungulates (Van Valen, 1978). Phenacodontid condylarths are close to ancestry of early perissodactyl as well as other ungulate orders (Van Valen, 1978). Dentitions of later perissodactyls can be derived from morphology like that in *Hyracotherium*.

Source : MNHN, Paris

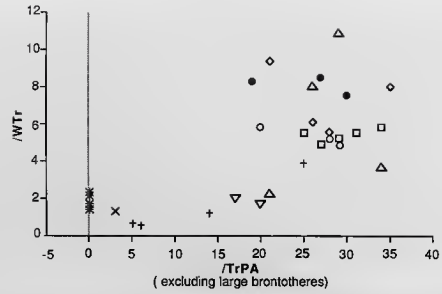

FIG. 7. — Scatter diagram of angle of posterior trigonid shear (/TrPA) versus width of lower molar (/WTr) in insectivores and herbivores except large brontotheres. /TrPA in degrees, /WTr in millimeters. For symbols, see Fig. 3.

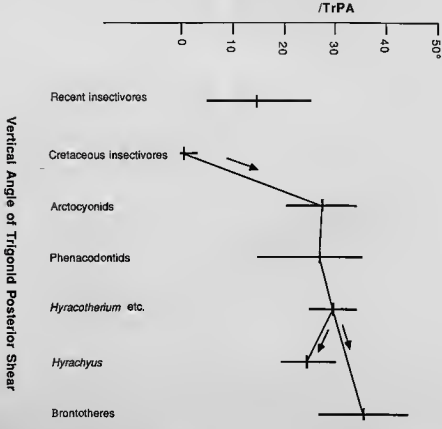

FIG. 8. — Differences in angle of posterior trigonid shear among different groups of ungulates compared to Cretaceous and Recent insectivores. See also legend of Fig. 6.

Source : MNHN, Paris

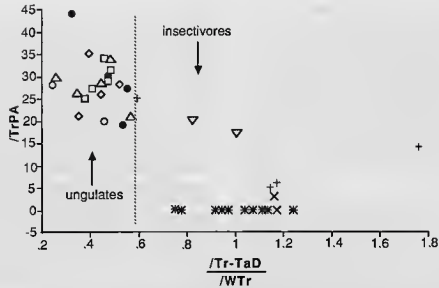

FIG. 9. — Scatter diagram of trigonid-talonid displacement (/Tr-TAD), as a fraction of tooth width (/WTr), versus angle of the posterior trigonid surface (/TrPA). See Fig. 3 for symbols.

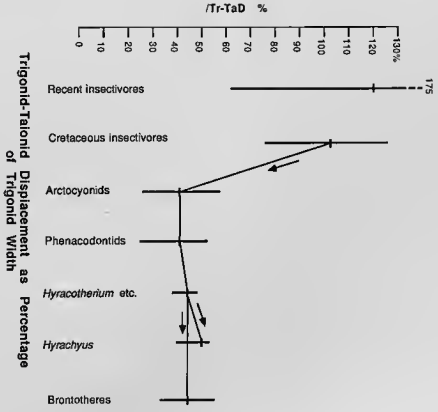

FIG. 10. — Differences in trigonid-talonid displacement as percentage of tooth width among ungulate groups compared to Cretaceous and Recent insectivores. See also legend Fig. 6.

Source : MNHN, Paris

values. There is an overall correlation (correlation coefficient = .73) between the relative depth of shear and the shear angle.

In the transition from the Cretaceous insectivores to the early ungulates, the relative decrease in shear displacement is great, almost 50 % of the tooth width (Fig. 10). After this transition, the change leading through the phenacodontids to the perissodactyls is negligible, although *Hyracchyus* shows a possible increase in the displacement.

Discussion

The results indicate that the transition from insectivore to herbivore was marked by a reduction in the taper of the cusps, reduction of the steepness of the trigonid shear surface, and reduction of the length of the shearing motion, as well as increase in size. Before attempting to interpret these changes, it is helpful to review several functional aspects that have previously been observed.

The Cretaceous insectivores tend to have a rather high chewing angle, between 23° and 35° from the vertical for the palaeoryctids (Butler, 1972; Rensberger, 1986). In the earliest ungulate, *Protungulatum*, the chewing angle is between 40° and 55°. (These estimated angles in these two studies differ by about 7°, owing to a difference in the method used to determine " vertical " in isolated teeth). In the phenacodontids the mean is about 57°, indicating a slightly lower chewing angle. In the early equid *Hyracotherium*, the angle is about the same as in the phenacodontids.

Both compressive and shearing modes of surface interaction occur as effective chewing mechanisms in insectivorous mammals. This duality is expressed as different chewing cycles (puncture-crushing, in which the food is crushed and punctured by the cusps without the teeth coming into close occlusion; and " chewing ", in which the teeth come into more intimate contact). These distinct modes have been observed in the opposum (Crompton & Hiiemae, 1970), the tree shrew and small primates (Hiiemae & Kay, 1973), the macaque (Luschei & Goodwin, 1974), man (Atkinson & Shepherd, 1961; Ahlgren, 1966, 1976), and the cat (Hiiemae & Thexton, 1975). It is also expressed as differences in wear on a single tooth, in which flat, oval shaped striae-less surfaces, indicating little translation, occur on the tips of the major cusps whereas striae occur on linear structures (crests) that join the major cusps (Rensberger, 1986).

In the early Tertiary periptychid and phenacodontid condylarths, the increased random directionality of the enamel edges and the expansion of the cusps suggest that the compressive mode became dominant (Rensberger, 1986). The perissodactyls inherited the phenacodontid pattern, but enhanced the shearing mechanism by increasing the linear alignment of certain structures (especially the ectoloph). In other words, these shearing mechanisms do not trace back to the vertical shearing of the insectivores, but were added to teeth in which most of the shearing structures had been lost.

The trend within the primitive herbivores for enlarged compressive surfaces and reduced shearing surfaces represents an extension of the trend at the insectivore-herbivore transition. The less vertical attitudes of the cusp and posterior trigonid surfaces, together with apical wear of the cusps, produced enlarged, flat occlusal surfaces (Fig. 11). The insectivore mechanism was dominated by sharply tapered cusps capable of penetration and shearing edges capable of slicing through insect carapaces. Owing to the difficulty of digesting cellulose (Rensberger, 1975: 20), a greater amount of mechanical exposure of individual cell interiors is required for efficient digestion of most plant parts. Mechanically smashing the plant to a thin pulp is probably more effective than slicing it into a few larger

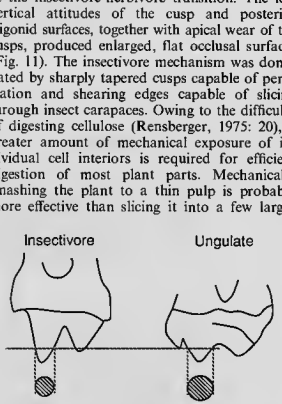

Fig. 11. — Effect of change in cusp taper angle on area of horizontal wear surfaces. Insectivore paracone has smaller facet area than paracone of ungulate after equivalent vertical distance of wear.

Source : MNHN, Paris

fragments, which is the effect of the few shearing edges in the insectivore molar. The insectivore teeth, with their interlocking tribosphenic morphology, are incapable of much horizontal translation, whereas that is the only way that successive parallel edges could be added to produce finer fragmentation by shearing. It is a relatively simple change, however, to increase the surface area of the existing compressive mechanisms, the tips of the cusps. The less vertical sides of the cusps then crowd out the crests that previously connected the cusps, resulting in smaller lengths of linear shearing structures and smaller percentages of the food that is processed by shearing.

Effects of size increase.

The increase in size that characterized the transition should be considered because some of the observed changes might be expected as a result of size increase alone. Cusps with less vertical sides are less fragile under transverse force and it is possible that this was a source of selection for less vertical surfaces. However, there is no evidence for a prominent change of chewing direction at the transition that would increase horizontal stress.

If cheek tooth occlusal area increased in proportion to the increased cross-sectional area of the masticatory muscles, there would be no increase in occlusal pressure. It is possible that relatively larger chewing muscles were selected to produce higher pressures for fracturing plant fibers, in which selection for heavier cusps would be needed to withstand higher compressive stress.

Another possibility is that, because of the much greater force available in a larger animal with proportionately larger muscles, even if the average occlusal pressure was not increased, there is the likelihood of stress concentration by small hard objects. However, the nearly vertical surfaces of the little changed tribosphenic teeth, such as were present in the early participants in the transition, would tend to shed hard objects rather than trap them between high pressure interfaces. It seems likely that stress concentration is a problem associated with surfaces of lower attitudes coming together in a movement perpendicular to the surfaces, and is therefore a problem appearing well after the transition to blunter cusps, not a selective factor producing the less vertical surfaces.

A possible result of stress concentration, however, was the acquisition of stronger enamel, and this was an event that occurred after the transition. Koenigswald, Rensberger & Pfretzschner (1987) found Hunter-Schreger bands, which are decussating layers of enamel prisms, in the early Paleocene arctocyonids but not in the late Cretaceous *Protungulatum*. This structure is size related, for it seems to be present in all Recent and extinct taxa with molars more than about 6 mm in width with one exception, the early Paleocene Periptychidae, and is absent in almost all non-rodent taxa smaller than that. The rare occurrences of H-S bands in modern insectivores are in incisor specializations in which the tooth is elongate and subject to high stress. In rodents, H-S bands are associated with the high stress developed in gnawing and chewing, especially in the incisors. Among the ungulates considered in this study, H-S bands are absent only in the very early *Protungulatum*. The presence of strengthened enamel in the subsequent larger ungulates is consistent with elevated chewing pressures that would result from stress concentration by hard objects and from relatively larger chewing muscles needed to pulverize tough vegetation.

Conclusion

The attitudes of contacting surfaces and the length of shearing movement during occlusion are simple dental characteristics that are fundamental to the occlusal mechanics of food fracturing. Most of the mammals studied can be classified as insectivore or herbivore on the basis of these characters. In the insectivores the sides of the paracone tend to taper at an angle of less than 50°, whereas only the most primitive of the ungulates has a paracone taper angle that low and in some the angle ranges over 80°. In the insectivores the posterior surface of the trigonid makes an angle with the vertical of less than 20° whereas in the early Tertiary ungulates studied the angle ranges from 18° to 45°. In all but one of the insectivores, the length of shear of the opposing molars is greater than 70 % of the molar width; in the primitive ungulates the length is less than 60 % of the molar width.

Source : MNHN, Paris

The changes in surface attitude and shear length in the transition to the ungulates represent increases in chewing surface area, flatter chewing surfaces, and reduced shearing motion between opposing surfaces. The effect of these changes to the masticatory occlusal mechanics was to shift the emphasis in food fracturing from a combination of translation (shearing) and compressive action, with shearing dominating, toward an increasing role for compression. The increase in size may have contributed to selection for larger cusps to prevent tooth breakage, but there is no evidence that it was the initial factor. A likely response to selection caused by tooth breakage, the appearance of Hunter-Schreger bands, did not occur before the other changes were well under way. In terms of timing and phylogenetic relationships, these changes began in the late Cretaceous *Protungulatum* and culminated within two of the major ungulate groups of the early and middle Paleocene, the Periptychidae and the Phenacodontidae, where the emphasis has shifted to compressive action. A translating type of movement between opposing surfaces reappeared in the dominant herbivores of the Eocene, the perissodactyls, which were descendants of the phenacodontids, but in a quite different morphologic context than that of the insectivore molars.

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Source : MNHN, Paris

Source : MNHN, Paris

An Estimation of Tooth Volume and Hypsodonty Indices in Ungulate Mammals, and the Correlation of these Factors with Dietary Preference

C. M. JANIS

ABSTRACT

Habitat preference appears to be more important than dietary preferenee in determining the degree of hypsodonty (tooth crown height) or dental volume in ungulate mammals. Ungulates feeding at ground level in open habitats are significantly more hypsodont (regardless of food preference) than ungulates living in closed habitats, and the lowest hypsodonty values are found in those ungulates feeding on dicotyledonous material above ground level. I suggest that the accumulated dust and grit on the food consumed in more open habitat areas is a more important variable in determining hypsodonty in ungulates than either the level of fibre in the diet, or the total amount of food consumed per day. However, total postcanine tooth volume may bear an important relationship with the latter factor, as grazing equids (hindgut fermenters) have a much larger dental volume than grazing ruminant artiodactyls (foregut fermenters) of a similar body size. Both individual and total postcanine tooth volume, and individual molar crown height in ungulate mammals are found to scale isometrically with body weight and to correlate with dietary type.

These data on living ungulates also provide a reference against which fossil ungulate species may be compared. Whilst all living species that are highly hypsodont are grazers, mere hypsodonty is not sufficient to determine diet. I suggest that other cranial proportions, for example relative muzzle width, may provide a better indication of dietary preference in conjunction with the degree of hypsodonty. In addi-

RÉSUMÉ

Le degré d'hypsodontie (hauteur de la couronne dentaire) ou le volume dentaire semblent davantage déterminés, chez les Ongulés; par la préférence pour un habitat donné que par la préférence pour un régime donné. Les Ongulés qui se nourissent au niveau du sol dans des habitats ouverts sont notablement plus hypsodontes (indépendamment des préférences alimentaires) que ceux qui vivent dans des habitats fermés, et les plus faibles valeurs d'hypsodontie se trouvent chez ceux qui se nourrissent de dicotylédones au-dessus du niveau du sol. L'auteur suggère que la poussière et le sable accumulés sur la végétation consommée dans les habitats plus ouverts jouent un plus grand rôle dans la détermination du degré d'hypsodontie chez les Ongulés que la quantité de fibres dans la nourriture, ou la quantité totale de nourriture consommée par jour. Cependant il se peut que le volume total des dents jugales ait une relation importante avec le dernier facteur, étant donné que les Equidés paisseurs (fermentation dans la partie postérieure du tube digestif) ont un volume dentaire bien plus grand que les artiodactyles ruminants paisseurs (fermentation dans la partie antérieure du tube digestif) de taille corporelle semblable. Le volume de chaque dent jugale comme celui de toute la rangée, et la hauteur de la couronne de chaque dent des Ongulés, ont un rapport isométrique avec le poids du corps et sont corrélatifs du régime dentaire.

Ces données chez les Ongulés actuels constituent aussi une base de comparaison pour les espèces

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) 53 : 367-387.

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Source : MNHN, Paris

tion, total postcanine tooth volume, in conjunction with other dental features, may serve to distinguish between foregut and hindgut fermenters in extinct ungulate lineages.

fossiles d'Ongulés. Bien que toutes les espèces vivantes qui sont hautement hypsodontes soient des paisseurs, la seule hypsodontie n'est pas suffisante pour déterminer le régime. L'auteur suggère que d'autres proportions craniennes, par exemple la largeur relative du museau, constituent une meilleure indication des préférences alimentaires en liaison avec le degré d'hypsodontie. En outre, il se peut que le volume total des postcanines, en liaison avec d'autres traits dentaires, serve à distinguer entre les animaux chez qui la fermentation s'opère dans la partie postérieure du tube digestif de ceux chez qui elle s'opère dans la partie antérieure, ceci dans les lignées d'Ongulés éteints.

Introduction

This paper documents the variation of postcanine tooth volume and tooth crown height (hypsodonty) with body size and dietary type over a wide range of species of living ungulate (hoofed) mammals. The incidence of high crowned cheek teeth, or hypsodonty, is seen in a number of living and extinct mammalian orders, and has generally been associated with a grazing habit (Simpson, 1950; McNaughton *et al.*, 1985). Yet the evidence for this has been largely qualitative rather than quantitative. Although one study has shown that opaline silica particles in grasses may contribute to wear in the teeth of sheep (Baker *et al.*, 1959), there has been no comprehensive study to date demonstrating a correlation between cheek tooth crown height and the abrasiveness of the diet in ungulate mammals. I present data from measurements of the majority of living ungulate species, (including X-ray measurements of hypsodont species). This large data set allows quantitative testing of the relationship between tooth crown height and dietary type. This paper deals exclusively with ungulates, although the conclusions from this paper may be applicable to all hypsodont mammals.

The term " hypsodont ", in referring to mammalian cheek teeth, is used in distinction from the terms " brachydont " and " bunodont ", which refer to low crowned teeth. That is, the regular mammalian condition where the base of the crown of the newly erupted unworn cheek tooth is visible at the junction of the tooth with the bone of upper or lower jaw. In hypsodont mammals, the base of the tooth is contained within the body of the jaw. That is, the tooth is elongated from crown to root over the normal mammalian condition and, as the tooth wears down during the course of the animal's lifetime, the tooth continues to erupt until the base of the tooth becomes level with the junction of the jaw. The term " hypsodonty " is usually used to describe a tooth in which the unworn crown height exceeds the anterior-posterior dimensions of the tooth (Mones, 1982).

The term " brachydont " and " bunodont " are sometimes used interchangeably in the literature, but in fact they refer to different aspects of tooth morphology. Cheek teeth may either consist of individual cusps (the primitive mammalian condition), or these cusps may be run together in various ways in specialized herbivorous mammals to result in lophed teeth. " Bunodont " refers to the tooth morphology of omnivorous or frugivorous mammals, where the individual cusps are low and round, as opposed to the high pointed condition of the cusps seen in the earliest mammals, and seen today in mammals with an insectivorous or carnivorous diet. Bunodont teeth are never hypsodont. The term " brachydont " refers to teeth in which the individual cusps are united into ridges or lophs, but which are not high crowned. " Hypsodont " refers to high crowned lophed teeth, and Fortelius (1985) suggested that the term " plagiolophodont " should be used to refer to those hypsodont lophed teeth that have a flat, rather than high ridged, occlusal relief (such as the type of tooth morphology seen in present day equids). The term " mesodont " is also frequently seen in the paleontological literature (Wood & Patterson, 1959), which refers to teeth that are somewhat more high crowned than the usually brachydont condition, but which are not considered to warrant the term hypsodont. A

Source : MNHN, Paris

final term, " hypselodont ", refers to those hypsodont cheek teeth which are rootless, and are thus evergrowing. These types of cheek teeth, common amongst present day rodents, are not found in any extant ungulate, although they were developed in certain extinct ungulate lineages, among the Rhinocerotidae and Notoungulata (Fortelius, 1985; Janis & Fortelius, in press).

Hypsodonty is usually interpreted as a response to increased dental wear (Van Valen, 1960; Romer, 1970; Fortelius, 1985). Previous workers (White, 1959) have interpreted hypsodonty as a device to increase the lifespan of animals of larger body size, but this hypothesis was laid to rest by Fortelius (1985), where he showed that there is no correlation between lifespan and degree of hypsodonty in living mammals. Fortelius discusses the fact that Simpson (1944, 1953) decided that hypsodonty in fossil equids was independent from body size increase in evolution, although the incidence of hypsodonty was spuriously correlated with size increase. (This is not suprising, as present day grazing hypsodont ungulates tend to be of medium to large body size, while brachydont browsers can be found in all size ranges). He contrasts this with the idea of Huxley (1953), who thought that the increased lifespan of larger animals would make high crowned teeth a necessity. In fact, both recent and fossil record evidence shows that ungulates of large body size can have brachydont cheek teeth (Janis, 1984).

The most comprehensive review on the incidence and causes of hypsodonty in ungulates is Fortelius (1985). He stresses that in theory hypsodont teeth may be related to a number of different factors, associated with the total amount of abrasion that the cheek teeth encounter during the lifespan of the animal. Simple abrasion may be caused by phytoliths in the diet (usually found in grasses), grit and other abrasive materials deposited on the food, or high occlusal stress. Increased abrasion may be encountered by the mastication of large quantities of low quality food, independent of the actual abrasiveness of the food itself (although in practice low quality food is likely to be abrasive in nature, for example fibrous grasses). Finally, increased food processing due to increased energy demands might also result in the evolution of hypsodonty. Thus, although hypsodonty is traditionally associated with a grazing habit, other functional demands besides a diet of fibrous grasses may lead to the evolution of hypsodont teeth.

Here I establish a standard listing of tooth crown height and postcanine tooth volume in the range of living ungulate species for comparison with other living mammals and with fossil ungulate taxa. The word " hypsodont " is often used in the paleontological literature, but there exists no standard reference to which one could address the question " as hypsodont as what? ". A case in point is the often quoted statement that certain North American camelids became hypsodont in the Miocene as the result of eating grasses in the newly formed savanna environment (Scott, 1937). There is no doubt that many Miocene camelids were more hypsodont than their Oligocene ancestors. Yet modern camelid species, which are in fact *more* hypsodont than the Miocene taxa (Janis, 1984) are not grazers, but fall into the category proposed in this paper of " mixed feeders in open habitats ". In fact, the camel species (genus *Camelus*) are only about as hypsodont as the similar sized eland (*Taurotragus oryx*), which is a bovid of similar dietary type. Similarly, the smaller llamas, (genera *Lama* and *Vicugna*), are more alike in hypsodonty measures to the similarly sized mixed feeding gazelline and rupicaprine bovids (Grant's gazelle, *Gazella granti*, and the chamois, *Rupicapra rupicapra*), than they are to the small grazing alcelaphine bovids such as the bontebok (*Damaliscus dorcas*) (Table 5). As long as "hypsodonty " is used as a relative, rather than as an absolute term, mistakes may be made in assessing the diets of fossil ungulate taxa.

Another concern of this study was to examine the differences between hypsodonty and total postcanine tooth volume. Hypsodonty is usually expressed as a dimensionless " hypsodonty index ", derived by dividing tooth crown height by some other linear variable. A significant difference may be found here in comparisons of foregut and hindgut fermenters. A hindgut fermenter will require a larger intake of food per day (and over its lifetime) than a foregut fermenter of similar body size and similar dietary type (Janis, 1976). My subjective observations from the variety of living ungulate taxa suggest that this compensation is met in hindgut fermenters by increasing total postcanine tooth area instead of, or as well as, increasing cheek tooth height, and this observation is confirmed in this study. Hindgut fer-

Source : MNHN, Paris

menting perissodactyls and hyracoids have large molarised premolars, whilst hypsodont grazing ruminant artiodactyls (foregut fermenters) actually decrease the size of the premolar row (Janis, in press).

The fact that hindgut fermenters have a larger total postcanine tooth volume than foregut fermenters was realized by Webb (1983) in his analysis of dietary type of Miocene North American ungulates, where he chose to look only at the volume of a single lower molar. Webb looked at the volume of M_1. I chose to examine the volume of M_3 in this study, as this is the only molar that is increased in size in certain "hypsodont" mammals (namely the wart hog, *Phacochoerus aethiopicus*, and the Oligocene stenomyline camelids). Webb's comparative study did not include suids, and he limited his comparisons with fossil ungulates to Miocene taxa, so his choice of M_1 was appropriate. However, I feel that M_3 is the most appropriate tooth to examine in this case of a more comprehensive comparative study.

A final concern of this study is the issue of the scaling of tooth height and tooth volume with body size. Pilbeam & Gould (1974) and Gould (1975) originally proposed that tooth dimensions should scale with metabolic requirements in mammals (i.e., with positive allometry). However, Fortelius (1985) refutes this hypothesis, by showing that dental measurements of length and area scale isometrically in almost all mammals examined. The only exception are cases of slight positive allometry in hystricomorph rodents (Pilbeam & Gould, 1974) and fossil hypsodont equids (Radinsky, 1984). However, to the best of my knowledge, the scaling relationships of tooth height and tooth volume have not been investigated prior to this study.

Material and Method

The data on average molar area (representing the sum of the averaged areas of all the postcanine teeth) were derived from a much larger data set on cranial and dental proportions in 127 species of living ungulates (from the orders Artiodactyla, Perissodactyla and Hyracoidea) (see Table 5 for list). The data on the elephant (*Loxodonta africana*) was compiled by Dr. Louise Roth from the paper by Laws (1966). The tooth measurements were taken as the length and width of the occlusal surface of the teeth, rather than as basal measurements. Work in progress by myself shows that tooth area measured in this manner does not change significantly with dental wear and increasing age of the animal, even though change does occur in the ratio of tooth length to tooth width. Nevertheless, the individuals selected from the data set for computation of average area of each postcanine tooth were limited to mature individuals (in which M_3 was fully erupted) that did not exhibit excessive dental wear.

These data were collected primarily from the Museum of Comparative Zoology (Harvard University, U.S.A.) and the British Museum of Natural History (London), but additional data were obtained from the Smithsonian Institution (the National Museum, Washington, U.S.A.), the National Museum of Kenya, the Transvaal Museum (Pretoria, South Africa) and the Cape Town Museum (South Africa).

Data were obtained on 127 species of living ungulates, including representative species of all ungulate genera. Tooth area measurements were obtained for at least 6 individuals of each species in almost all cases, although the estimates of tooth crown height were done on a more limited number of species, as will be shortly explained.

In estimating total tooth volume (taken as the total tooth volume in one lower jaw) I attempted to derive an estimate of the total dental volume available to an animal for its adult lifespan. This involved the measurement of the unworn height of each permanent tooth in the lower jaw, and an estimation of the occlusal surface area. Work in progress by myself has shown that in adult ungulates, although the length and width measurements may change as the tooth is worn down, the occlusal area remains more or less constant. However, as a precaution, length and width measurements were taken only from adult animals (that is, with all teeth erupted) that showed slight to moderate tooth wear. Crown height was taken as the distance from the base of the crown to the tip of the protoconid. Tooth length and width were both measured on the occlusal surface of the tooth: length was measured as the maximum labial excursion of the tooth; width was measured between the outer surfaces of the protoconid and the entoconid.

Ideally, I would have included the volume of

Source : MNHN, Paris

the deciduous teeth in this estimation, but such data are impossible to obtain for the range of species in this comparative study. It is obviously impossible to estimate total unworn tooth volume from a single individual. In most ungulate species, by the time the second and third molars have erupted, the first molar already exhibits signs of considerable wear. Thus a minimum of two individuals were used to estimate tooth volume; one young individual in which M_1 had just erupted, and one slightly older individual in which M_2 and M_3 had erupted but were not yet worn. In almost all cases, different individuals were used for the measurement of the height of M_2 and M_3. For a very few species (indicated on Table 5) only one specimen of a young adult (with a worn M_2) was available for study. In these cases the height of M_1 was estimated as being approximately 5 % less than the unworn height of M_2 (which was seen to be the case in the other species when unworn height of both teeth could be measured directly). It must be emphasised that, in Table 5, where the " no. of individuals " measured for estimates of tooth height is listed as " 1 ", in almost all cases this refers to the minimum number of height estimates for *each tooth*, meaning that at least two, and more usually three or four, individuals of that species were measured in order to obtain height measures for each tooth in an unworn condition.

X-rays were taken of all species in which the teeth were sufficiently hypsodont that it was not possible to see the base of the tooth in the unworn condition (see notation in Table 5). All X-rays were taken at the British Museum of Natural History, from specimens in their collections. Although ideally it would have been preferable to use X-rays to measure unworn tooth height in a large number of individuals of each species, in practice such data are almost impossible to obtain. When selecting specimens for X-ray, it was difficult to find even one suitable specimen of each age stage in many cases (that is, of a young adult, with unworn permanent teeth), even in the large collection of the British Museum. Museum collections are biased towards younger or older individuals, as these are the ones that are the most likely to die from natural causes (or, in the case of older individuals of horned ungulates, are the ones that were shot as trophies.) The data collected for the more brachydont species suggest that the variation in maximum unworn tooth height within a species is minor compared to the variation between species.

The tooth volumes presented in this paper were derived treating each tooth as an elongated cube, multiplying length, width and height dimensions obtained as previously described. The actual dental volume for a species was calculated by multiplying the average area for each tooth by the average of the estimates for the unworn height of that tooth, and the values for each tooth in one lower jaw half were then summed. As the tooth volume estimated by this method was a composite measure derived from a number of individuals, it was not possible to obtain a realistic estimate of the standard deviation for this value. The range of values portrayed in Table 5 are again composite values. The minimum or maximum volume was obtained by summing the minimum or maximum values for each tooth. These individual tooth values were obtained by multiplying the minimum (or maximum) area by the minimum (or maximum) unworn crown height. I would expect that the ranges obtained in this fashion are rather larger than would be exhibited in actual individuals of the various species, and suggest that these should be treated as a guide rather than as absolute values.

Hypsodonty index was determined as M_3 height divided by M_3 width. The rational for this is as follows. Despite Van Valen's (1960) assertion that the linear measurements used to devise a relative measure of tooth crown height should not be taken from other molar measurements, a hypsodonty index derived solely from dental measurements is more practical, for comparison of living and fossil taxa. In many cases dental remains are the only positively identifiable remains for fossil ungulate species. A hypsodonty index derived from a division of molar height by molar length would be misleading in the case of certain taxa. For example, the third lower molar is usually the tooth with the greatest crown height in ungulates, and is the only significantly highly crowned tooth in certain hypsodont taxa (for example, in the case of the wart hog and the extinct stenomyline camelids). However, in the previously mentioned taxa, M_3 is also greatly elongated, and so a division of M_3 height by M_3 length would not reveal the fact

Source : MNHN, Paris

that this tooth was exceedingly high crowned. I tried to circumvent this problem in a previous paper (Janis, 1984), when I devised a hypsodonty index for ungulates from M_3 height divided by M_2 length. This had the advantage of an intuitively " obvious " value of one as the point when tooth crown height exceeded average molar tooth length, above which value teeth might be defined as hypsodont (Mones, 1982). The problem with this measurement is that it would not work in the case of elephants, in which every tooth is greatly elongated, nor in the case of suids, where the last molar is greatly enlarged in length. Thus I consider the definition of the hypsodonty index presented here to be the most practical compromise for the comparison of a wide range of living and fossil ungulate taxa, especially as a fossil animal might only be represented by a single tooth, rather than by a complete or partial lower jaw. (A hypsodonty index derived from any unworn molar would bear a good approximation to that derived from M_3 in most cases.)

The body weights used in this study were derived from a number of sources. The body weights for bovids were taken from Scott (1983) and those for cervids were taken from Scott (1987). Body weights for the other ungulate species were taken from Walker (1983) or Macdonald (1984). The body weights cited in Table 5 are the average of the body weights for the males and females of the species. The data set that generated the average postcanine tooth areas was comprised of approximately equal numbers of males and females for each species. In addition, there is little evidence of sexual dimorphism in cheek tooth area in ungulates, even in species that are highly sexually dimorphic (Fortelius, 1985; Janis, in preparation).

The dietary divisions used in this paper were derived from those of Hofmann & Stewart (1972). They divided grazing ungulates (defined as those species taking at least 90 % of their year round diet in the form of monocotyledonous grass material) into " roughage grazers ", " fresh grass grazers dependent on water " and " dry region grazers ". My category " F " or " fresh grass grazer " in this paper corresponds to their fresh grass grazer category, and my " grazer " category " G " lumps together the other two types of grazers. Hofmann & Stewart divided browsing ungulates (defined as those ungulates which select " juicy, concentrated dicotyledonous herbage " as at least 90 % of their diet) into " tree and shrub foliage eaters " and " fruit and dicot foliage selectors ". The latter category corresponds to my category " S " or " selective browser ". The former category is split into two in this study. Those browsers which almost invariably feed above ground level are classified as " H " or " high browsers ", and the other browsers feeding both above the ground and at ground level are categorised as " B ", or "regular browsers ". The rational for this split was the empirical observation that high browsing ungulates appeared to be less hypsodont than other browsers, an observation that has been confirmed in this study. Hofmann & Stewart also had a category of " intermediate " feeders, with variable diets. They split this category into those " preferring grasses ", and those " preferring forbs, shrub and tree foliage ". These categories approximately correspond to my division of " mixed feeders in open habitats " (" M "); that is, living in savanna or prairie; and " mixed feeders in closed habitats " (" W "); that is, living in bushland, woodland or forest. My reasons for dividing mixed feeders by habitat type rather than by percentage of grass in the diet was again the result of empirical observations. For example, the pronghorn (*Antilocapra americana*) is a mixed feeder living on the western American prairies. Despite the fact that it only takes a small percentage of grass in its diet (Olsen & Hanson, 1977), it has highly hypsodont cheek teeth. Thus habitat was taken as a more preferable category for the division of the mixed feeders than the percentage of grass in the diet. Finally my category " O ", or " omnivore ", used only in the case of certain suine species, referes to those animals which take a considerable proportion of roots and animal matter in their diet, in addition to fruit and other types of vegetation.

The information on diets and habitats of the various species (Table 5) was obtained from the following sources. Hofmann & Stewart (1972) and Kingdon (1979, 1982a and 1982b) were used for the African ungulates; Schaller (1967 and 1977) was used for the Asian artiodactyls; Hansen & Clark (1977) and Olsen & Hansen (1977) were used for the North American ungulates; Whitehead (1972) was used for the European and South American cervids; Walker *et al.* (1978) was used for the hyraces; when all other

Source : MNHN, Paris

sources failed, reference was made to Walker (1983).

Results

Fig. 1 shows a plot of hypsodonty index in living ungulates against the logarithm of body weight. Although there is a wide amount of scatter, it is intuitively obvious that the grazers (" G " and " E ") are the most hypsodont of the feeding types, although many mixed feeders in open habitats (" M ") are as hypsodont as some of the grazers. The equids (" E ") stand out as a distinct cluster of highly hypsodont grazers. The one included elephant species, the African elephant (*Loxodonta africana*), does not stand out as especially hypsodont in this plot. The grazing rock hyrax, *Procavia capensis*, has a very low hypsodonty index for a grazer, but this probably reflects the fact that hyraces have an unusually low metabolic rate for their body size (Taylor & Sale, 1969). The fresh grass grazers (" F ") appear to have a considerably lower hypsodonty index than the other grazers. The mixed feeders in closed habitats (" W ") are considerably less hypsodont than the mixed feeders in open habitats, and are only slightly more hypsodont than the majority of browsers of all types (" B ", " S " and " H "). The small bovids that are browsers (" B ") and selective browsers (" S ") appear to be abnormally hypsodont for their dietary type (Fig. 1), but this may be an artifact of the fact that hypsodonty does not usually appear to be decreased in evolution once it has evolved (Fortelius, 1985). The small bovids are probably secondarily small (Janis, 1976), and may have secondarily reverted to browsing from a mixed feeding diet that required a greater degree of

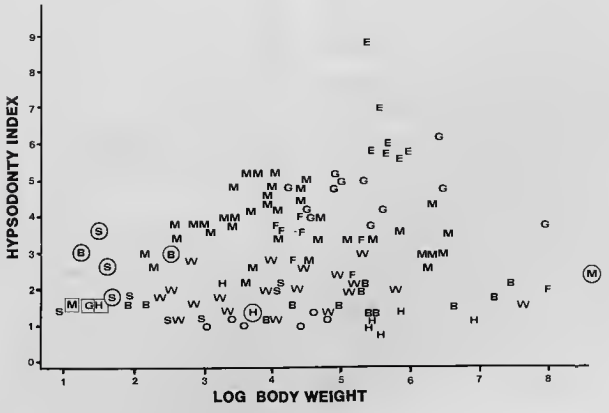

FIG. 1. — Plot of Hypsodonty Index against Log. Body Weight.
Letter abbreviations for dietary types as for Table I.
(S) or (B) indicate small browsing bovids (Cephalophini and Neotragini). E indicates equids (all grazers). (M) the elephant, *Loxodonta africana*. (H) is the gerunuk, *Litocranius walleri*. □ around letter indicates hyrax species.

Source : MNHN, Paris

hypsodonty. One exception to the rule that hypsodonty is not secondarily reduced may be the gerunuk, *Litocranius walleri* (Fig. 1), which is a high browsing gazelle that has an exceptionally low hypsodonty index for a bovid. The feeding types with the lowest index of hypsodonty appear to be the omnivores and the high browsers.

Statistical examination of the means of the hypsodonty indices produced the following results (Table 1). Considering all ungulate taxa (Table 1A), grazers were significantly different from all other feeding types, with the greatest mean hypsodonty index ($P < 0.05$). Mixed feeders in open habitats and fresh grass grazers, with the next highest mean hypsodonty indices, could not be distinguished from each other. But fresh grass grazers and selective browsers can be united together in a group that can be distinguished both from grazers and mixed feeders in open habitats on the one hand (mean hypsodonty index significantly less), and from all other feeding types on the other (mean hypsodonty index significantly greater). Finally, no distinction is possible between the mean hypsodonty indices of mixed feeders in closed habitats, omnivores, and browsers of all types.

The significance of the variation of the hypsodonty index with dietary type was reexamined with a subset of the total species data (Table 1B). This subset eliminated the following types of ungulates: equids (because of their exceedingly high levels of hypsodonty, that I thought might act to bias the overall value of the hypsodonty index for non-equid grazers); elephants, because of their unique mode of sequential tooth replacement (Laws, 1966); hyracoids, because of the possibility that their low metabolic rate was contributing to their extremely low hypsodonty values; and the small hypsodont browsing bovids, which were judged as possibly being " abnormally hypsodont " for their body size, as previously discussed. (With the removal of the bovids, the only ungulates remaining in the " selective browsing " category are the tragulid species).

In this analysis, grazers are still significantly different from all other feeding types, and mixed feeders and fresh grass grazers still group together. However, the selective browsers now have a lower mean hypsodonty index than mixed feeders in closed habitats and regular browsers, and none of these dietary types (including high browsers) can be distinguished from each other. However, mixed feeders in closed habitats can be distinguished as having a higher mean hypsodonty value than omnivores.

Another subjective observation from this plot is that, within certain feeding types (especially the browsing types, and in the mixed feeders in open habitats), the hypsodonty index appears to be greater in small animals than in larger ones. Regression lines (plotted by the least squares method throughout this study) were calculated for the hypsodonty index of each dietary type against log body weight. While there appeared to be a definite negative trend in the case of all the browsers, in the mixed feeders in open habitats and the fresh grass grazers, none of these regression lines were significantly different from zero. Thus it cannot be proven that smaller ungulates tend to be more hypsodont than larger ungulates of the same feeding type. However, the trend obviously has some reality, and I would caution people comparing hypsodonty indices of fossil ungulate taxa with living species to choose taxa of approximately the same body size for comparison. The scatter in this plot was considered to be too great to attempt a mathematical analysis of the significance of differences in hypsodonty indices with feeding type, as a regression line plotted through all these points would be almost meaningless. However, this type of mathematical analysis was performed with other dental variables, as detailed below.

Figs. 2-4 and Tables 2-4 show the results of the regression of log. total postcanine tooth volume, third lower molar height and third lower molar volume respectively against log. body weight. Analysis was made of pairwise comparisons of residuals for the different feeding types from the overall regression line. The test of significance used in each case was the T-test derived for the Wilcoxon scores from a 2-sample test with normal approximation (the data were analysed using the SAS statistical package).

In examining the analysis of the significance in the differences between the residuals, I decided to use a subset of the species data for the calculation of both the regression line and the residuals. In the case of the regression of total postcanine volume and third lower molar height against body weight, the data used were for artiodactyls and non-equid perissodactyls. In the case of the regression of third lower molar volume against body weight, the data used were for all ungulates

Source : MNHN, Paris

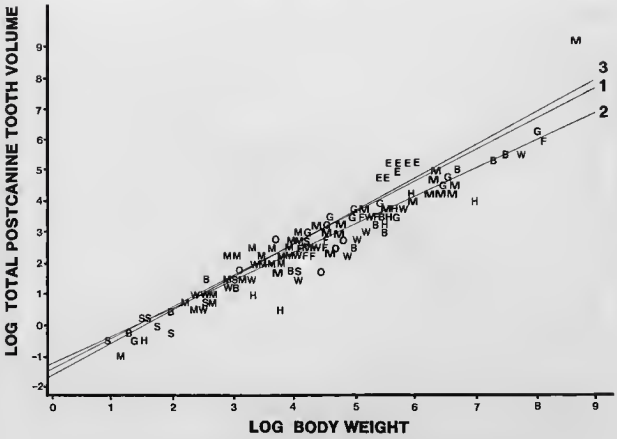

FIG. 2. — Plot of Log. Total Postcanine Tooth Volume against Log. Body Weight.
Key for dietary types as for Table 1.
Values for regression lines:
1. All taxa (except elephants): Intercept = -1.467. Slope = 0.955. r^2 = 0.904.
2. Artiodactyls and non-equid perissodactyls: Intercept = -1.275. Slope = 0.898. r^2 = 0.92.
3. All taxa: Intercept = -1.579. Slope = 0.984. r^2 = 0.903.

with the exception of elephants and hyracoids (however, the figures contain the information for the regression lines on the total data set).

The rational for this decision was as follows. The elephant is clearly highly specialized in a different way from other ungulates, in the peculiar method of tooth replacement, utilizing only one enlarged tooth in each jaw half at any one point in its lifespan (Laws, 1966). It cannot be imperative that an ungulate of this body size *must* adopt this morphological strategy in order to generate sufficient tooth volume for its lifespan, as the deinotheres (Old World, Tertiary and Pleistocene, apparently browsing proboscideans) were of similar size to present day elephants, yet had the normal mammalian pattern of tooth replacement (Harris, 1975). However, Pleistocene proboscideans in the families Mammutidae and Stegolophodontidae paralleled elephants both in the acquisition of hypsodont, lophodont molars, and in their mode of tooth replacement (R. Graham, pers. comm.; J. Shoshoni, pers. comm.). Thus the living elephant represents a specialized case that might act to strongly bias the data on other ungulate species. As previously detailed, living hyraces have abnormally low metabolic rates for their body size, and thus might also act to bias the total data set in the opposite direction.

Finally, I excluded the equids from the regression line in the first two plots, as they clump together as an outstandingly hypsodont assem-

Source : MNHN, Paris

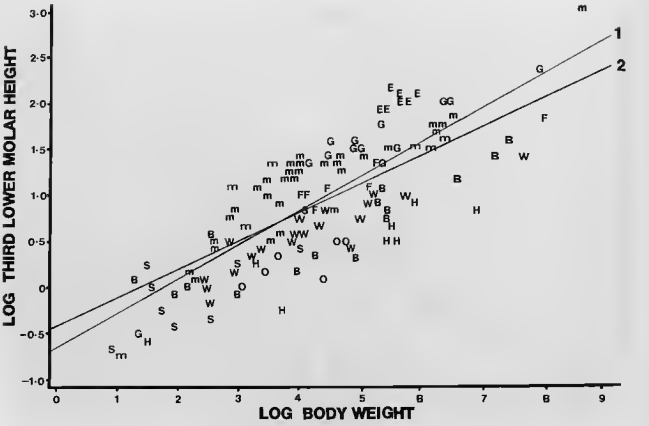

FIG. 3. — Plot of Log. Third Lower Molar Height against Log. Body Weight.
Key for dietary types as for Table 1.
Values for regression lines:
1. All taxa (except elephants): Intercept = -0.647. Slope = 0.355. r^2 = 0.63.
2. Artiodactyls and non-equid ruminants perissodactyls: Intercept = -0.465. Slope = 0.306. r^2 = 0.56.

blage (I wanted to see if grazing ruminants could still be distinguished from other dietary types without the "equid pull" to bias the data). However, in the plot of third lower molar volume against body weight, equids appear to be indistinguishable from grazing ruminants of a similar body size (as originally observed by Webb (1983)).

Fig. 2 illustrates the plot of log. total postcanine tooth volume against log. body weight, and Table 2 displays the extent of significant differences between a pairwise comparison of the residuals of the different feeding types around the regression line. The slope of the line, when all taxa are included, is 0.98, the slope of the line for ungulates minus elephant is 0.955, and the slope of the line for only artiodactyls and non-equid perissodactyls is 0.898. All slopes are significantly different from 0.0 ($P < 0.001$), none different from 1.00 ($P > 0.05$), and they are all significantly different from a slope of 0.75 ($P < 0.0001$). All lines indicate an isometric or near isometric scaling of total postcanine tooth volume to body weight. The fact that the line which includes all ungulates is a slightly better approximation to isometry suggests to me that perhaps there is a real adaptative advantage to the elephant mode of tooth replacement for an ungulate of very large body size, but discussion of this possibility is a matter for future research, rather than for this paper. The r^2 values (0.903, 0.904 and 0.92 respectively) are high, considering the fact that one would expect a certain amount of scatter around the regression line when comparing animals of different dietary types.

Pairwise comparison of the residuals around the regression line (Table 2) shows that the grazers (with the highest residual values) are

Source : MNHN, Paris

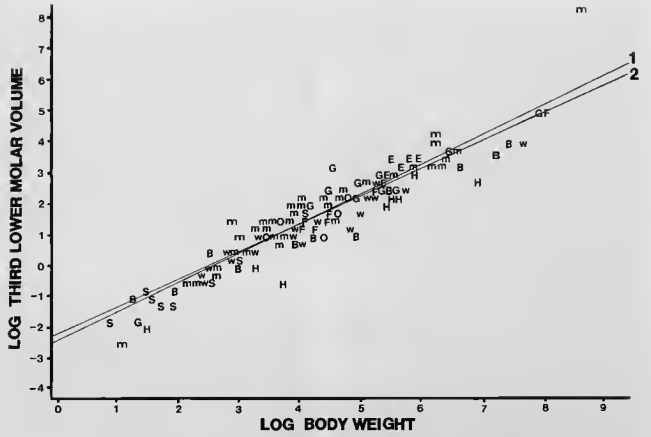

FIG. 4. — Plot of Log. Third Lower Molar Volume against Log. Body Weight.
Key for dietary types as for Table 1.
Values for regression lines:
1. All taxa; Intercept = -2.55, Slope = 0.965. r^2 = 0.89.
2. All taxa except elephants and hyracoids; Intercept = -2.25, Slope = 0.896. r^2 = 0.89.

significantly different ($P < 0.05$) from all feeding types, with the exception of mixed feeders in open habitats and omnivores. Fresh grass grazers are significantly different from regular grazers and mixed feeders in open habitats (lower tooth volume) ($P < 0.05$), but cannot be statistically distinguished from other feeding types. Mixed feeders in open habitats are significantly different (greater tooth volume) ($P = 0.05$ or less) from mixed feeders in closed habitats and all browsers. No significant difference can be discerned between any of the other feeding types, although the value of the residuals for the high browsers is the lowest of any feeding type.

Fig. 3 and Table 3 illustrate the plot of log. third molar height against log. body weight, and the values for the residuals of the feeding types around the regression line. The slope of the regression line is 0.355 in the case of all ungulates, and 0.306 in the case of the artiodactyls plus non-equid perissodactyls. Although both slopes differ significantly from 0.0 ($P < 0.001$), neither slope is significantly different from 0.33 at the 0.05 confidence level. In a comparison of a linear measurement with a volumetric one, the expected slope for an isometric scaling relationship would be 0.33, so near isometric scaling of linear dental dimensions is again validated.

Significant differences ($P < 0.05$ or less) are found between all feeding types with the exception of the following combinations: grazers cannot be distinguished from mixed feeders in open habitats, although the value of the grazing residuals is higher; mixed feeders in closed habitats, selective browsers and regular browsers cannot be distinguished from each other, although

Source : MNHN, Paris

high browsers have residual values that are significantly lower than all other browsing feeding types; omnivores cannot be distinguished from any type of browser, but the value of the omnivore residuals is significantly lower than for any type of grazer or mixed feeder.

The significance of the third lower molar height in predicting dietary type was examined in two additional ways. The dietary types were grouped into " open habitat " types (comprising grazers, fresh grass grazers and mixed feeders in open habitats) and " closed habitat " types (comprising all the other categories). There was a sign difference ($P < 0.001$) between the two residuals (" open " = 0.29, " closed " = -0.35). A comparison was also made between " grazers " (grazers plus fresh grass grazers), " mixed feeders " (in both open and closed habitats) and " browsers " (all other feeding types). The residuals of " grazers " (0.33) and " mixed feeders " (0.10) were significantly different ($P < 0.01$), and both " grazers " and " browsers " (-0.40), and " mixed feeders " and " browsers " were significantly different from each other ($P < 0.0001$).

Finally, Fig. 4 and Table 4 illustrate the plot of the log. of the third lower molar volume against log. body weight, and a comparison of the residuals by feeding type around the regression line. Here, as for the plot of the entire postcanine volume, the slopes of the lines (0.965 for all ungulates, 0.896 for all ungulates except elephants and hyracoids) indicate a near isometric scaling of the volume of a single molar with body weight. Neither of these slopes is significantly different from 1.00 ($P < 0.05$), and they are both significantly different from 0.75 ($P < 0.0001$) confidence level. One problem with this particular analysis is that all suines (which are the only members of the omnivore dietary category) have a somewhat enlarged third lower molar area. Suines exhibit a certain amount of horizontal replacement of the tooth row during life, with the full area of M_3 only coming into occlusion once the anterior molars have been considerably reduced in size by wear (Cooke & Wilkinson, 1978). As a result, omnivores cannot be distinguished from any other feeding category in a pairwise comparison of residuals. However, with the exception of this dietary category, the results of the pairwise comparison of the residuals around the regression line is as follows: grazers are distinguishable from all feeding types ($P < 0.01$ or less), with the exception of mixed feeders in open habitats. Mixed feeders are distinguishable from all feeding types except grazers and fresh grass grazers ($P < 0.05$). Fresh grass grazers can be distinguished only from grazers, high browsers and mixed feeders in open habitats. No distinction is possible between mixed feeders in closed habitats, browsers, selective browsers and fresh grass grazers. High browsers can be distinguished from mixed feeders in closed habitats and regular browsers ($P < 0.05$), but cannot be distinguished from selective browsers, although once again the mean value for the residuals for high browsers is lower than that for any other dietary type.

Discussion

It is apparent from the results presented here that both total postcanine and individual molar volume and individual tooth crown height scale isometrically with body weight. These data add to the list of dental dimensions presented by Fortelius (1985) that scale isometrically with body weight. As Fortelius (1985) points out, there is a conceptual problem with isometric scaling of dental measurements, in the light of the fact that most physiological processes in mammals (including ingestion rate) scale as body weight to the threequarter power ($B.W.^{3/4}$) (Peters, 1983). However, Fortelius overcomes Gould's assertion (1975) that isometric represents only functional similarity by an ingenious solution (Fortelius, this volume). Fortelius further suggests that this hypothesis of a functional basis for isometric scaling of dental proportions could be easily tested. He suggests that non-isometric scaling would be found when the diet consisted of food which could not be manipulated as a plastic mass during chewing, when the time of feeding was restricted, and/or when chewing rate did not scale as $B.W.^{-1/4}$. Data presented by Fortelius suggest that there may indeed be differences in dental scaling in relation to body weight between ungulates and carnivores, relating to the different nature of the type of food comminuted.

It is also apparent that both tooth crown height (hypsodonty), and total postcanine or individual molar volume, can distinguish among ungulates of different dietary type. Hypsodonty

Source : MNHN, Paris

(which could be expressed simply as tooth crown height or as a dimensionless hypsodonty index) appears to be the best significator in determining dietary type, as this variable produced the greatest number of significant differences between animals grouped by dietary type. However, some interesting conclusions can be derived from the tests of the ability of dental dimensions to predict diets in ungulates.

Although grazers appear to score higher than mixed feeders in open habitats on all tests of the correlation of tooth dimensions with dietary type (that is, they exhibit greater total or individual tooth volume, or greater tooth crown height or hypsodonty index), only the hypsodonty index demonstrates a significant difference between these dietary types. All other tests show grazers and mixed feeders in open habitats to have significantly greater dental dimensions than fresh grass grazers and mixed feeders in closed habitats, although fresh grass grazers can only be distinguished from mixed feeders in closed habitats by virtue of a greater hypsodonty index or M_3 height. Mixed feeders in closed habitats cannot be distinguished from regular or selective browsers in any tests, despite the fact that the mean values for these mixed feeders are higher than for browsers for most dental variables. In contrast, high level browsers can be distinguished from both other browsing types in the case of M_3 height, and from regular browsers in the case of M_3 volume, although the mean values for high level browsers are consistantly lower than for any browsers. With the exception of hypsodonty index, the mean values for high level browsers are also lower than those of the suine omnivores.

If one were to set up two contrasting hypotheses, namely that fibrous grasses in the diet were the most important factor in determining the level of hypsodonty of the cheek teeth, or that the grit accumulated on the food was the most important factor, one would expect the following contrasting results. If a diet of grass was the most important, one would expect all grazers, regular or fresh grass grazers, to be the most hypsodont. Mixed feeders in all habitats, would be expected to have a lower value of hypsodonty than all grazers, but a higher value than all browsers and omnivores. Finally, all browsers and omnivores would be expected to have a similarly low value of hypsodonty. However, if grit was the determining factor, one would expect all species feeding at ground level in open habitats, regardless of dietary preference, to have high hypsodonty values, and fresh grass grazers would be expected to have a lower value than other grazers, perhaps due to the muddy, rather than dusty, environment in which they forage. Mixed feeders in closed habitats would be expected to have a similar low value of hypsodonty to browsers feeding at ground level, regardless of the degree of fiber in the diet (i.e. regular browsers would exhibit similar values of hypsodonty to selective browsers or omnivores). However, high level browsers would be expected to have the lowest values of hypsodonty, as grit would be least likely to accumulate on above ground plant structures.

The results presented here clearly support the second hypothesis, and lead me to the conclusion that the most important issue in determining hypsodonty is the grit and other abrasive material accumulated on the food that must be ingested by the animal during feeding. Fresh grass grazers consume grass in similar quantities to regular grazers, although the fibre level of the grass is likely to be lower than for regular grazers (Hofmann & Stewart, 1972), and in their near water habitat they would be expected to encounter food that was relatively free of accumulated dust and grit. However, their hypsodonty values are lower than those of the mixed feeders in open habitats, which may consume little grass material, and ingest a diet that is less fibrous in quality than fresh grass (hence needing a smaller intake per day). However, mixed feeders in open habitats would be expected to consume considerable amounts of dust and grit along with the food. Likewise, mixed feeders in closed habitats would be expected to encounter less grit on the food than the mixed feeders in open habitats, and their dental dimensions are usually indistinguishable from those of most browsers, despite the fact that they may include a considerable proportion of grass in their diet. Finally, the lowest values for all dental dimensions are seen in the high level browsers. Although the fiber level of the food of high level browsers may be similar to that of regular browsers, it may be assumed that less dust and grit would accumulate on plant structures that were sufficiently above ground level to necessitate browsing at "head height".

The conclusion that grit is the most important factor in determining the degree of hypsodonty in ungulates does not necessarily mean that the

Source : MNHN, Paris

abrasive nature of grass ingested, nor the greater intake necessitated by the consumption of a fibrous diet, have no role in determining the degree of hypsodonty or the dental volume. There is no doubt that siliceous particles contained in grasses may result in dental abrasion (Baker *et al.*, 1959), and McNaughton *et al.* (1985) have suggested that coevolution between herbivores and grasses has taken place over time to result in higher concentrations of silica as a plant defence mechanism in heavily grazed areas, such as in the African Serengeti region. Coevolutionary events of this nature may have led to the evolution of the extremely high crowned teeth seen in many grazers (especially in the Equidae), and it is apparent from the data presented here that grazers are somewhat more hypsodont than mixed feeders in open habitats, even if these differences cannot be shown to be statistically significant by all tests employed. However, these data do imply that the preferred habitat of the animal plays a more significant role than the actual nature of the diet in determining tooth height and dental volume, and that "hypsodonty" alone cannot be taken as being diagnostic of a grazing habit in an ungulate species.

This conclusion may explain why certain primate and marsupial species that eat grass in open habitats, such as some baboons and large kangaroos, do not have markedly hypsodont cheek teeth. Unlike ungulates, these mammals are able to use their forelimbs to aid in the selection and manipulation of food items, and may be able to discard accumulated dust and grit prior to ingestion. Tooth crown height taken in isolation cannot be considered as a reliable sole determinant of dietary type in extinct mammals, and additionally mammals may countenance abrasive diets by other means than hypsodonty (see Janis & Fortelius, in press). However, other cranial measurements may enable the distinction between grazers and mixed feeders in open habitats. For example, there is a significant difference in the ratio of muzzle width to palatal width between ungulates of different dietary types. Mixed feeders and browsers are more selective in their food intake than grazers, and have relatively narrower muzzles (Janis & Ehrhardt, in press). (See also Janis, in press, for other factors.) Microwear on the teeth (Walker *et al.*, 1978), and patterns of gross dental wear (Kay, 1978; Janis, 1979), may also serve as a way determining diets in fossil taxa.

In summary, I would draw the following parameters from the values of the hypsodonty index presented here (i.e., M_3 height divided by M_3 width) (Tables 1 and 5). (These parameters are obviously approximate ranges rather than rigid divisions, and care should be taken to consider the body size and the taxonomic associations of the animal in question, as previously discussed.) The term "brachydont" should be restricted to ungulates with a hypsodonty index of less than 1.5. The term "mesodont" should be applied to ungulates with a hypsodonty index ranging between 1.5 and 3, and the term "highly hypsodont" might be applied to those hypsodont species with hypsodonty indices of a greater value than 4.75. Almost all living ungulates that fall into the "highly hypsodont" category are grazers, although a few mixed feeders in open habitats have higher hypsodonty values, and some regular grazers may have a lower hypsodonty indices (for example the hippotragine grazing bovids, and the white rhinoceros). All fresh grass gazers have a lower index of hypsodonty, some even falling into the "mesodont" range. For ungulates in the "regular hypsodont" range, relative muzzle width may prove to be a useful means of distinguishing grazers of all types from mixed feeders in open habitats.

However, in using Table 5, it should be noted that the point of this study is to compare a large number of different species in order to obtain a comparative estimation of how molar dimensions vary with body size and dietary type, rather than to provide an accurate estimate for each individual species for comparison with closely related species. For example, the data presented here suggest that the African camel (*Camelus dromedarius*) is slightly less hypsodont than the Asian camel (*Camelus bactrianus*). But I would not propose on the basis of this data set that this detailed between-species comparison should be taken as significant, requiring a functional or adaptive explanation, as the examination of more individuals of each species might result in slightly different estimates. However, the data points as presented provide information of hypsodonty levels of large camelids for comparison with the range of other ungulate species. Detailed comparisons between closely related species would require more extensive investigation. Likewise, the wide range of hypsodonty values for any given feeding type (Tables 1 and 5) should act as

Source : MNHN, Paris

a caution to anyone trying to determine the feeding type of the animal from the hypsodonty index alone.

A final observation is that hindgut fermenters appear to have a larger total postcanine tooth volume than foregut fermenters of similar body size. This is especially true for equids. A case in point here is a comparison of the common zebra (*Equus burchelli*) and the wildebeest (*Connochaetes taurinus*). The classic study by Bell (1971) showed that these similar sized species have a similar diet in the Serengeti savanna, although the wildebeest selects somewhat less fibrous parts of the grass plant. A comparison of hypsodonty indices of these species accords with this observation, as the zebra has a hypsodonty index of 5.83 in comparison to the hypsodonty index of the wildebeest of 4.94. Yet a comparison of total postcanine tooth volume shows a value of 111.92 cc for the zebra in contrast to 49.08 cc for the wildebeest! (Table 5).

As mentioned previously, hindgut fermenters (perissodactyls, hyracoids and proboscideans) have large, molarised premolars, that are of similar crown height to the molars. In contrast, foregut fermenters (ruminant and tylopod artiodactyls) have smaller premolars that are lower crowned than the molars in the case of hypsodont animals (the omnivorous species of the suoid artiodactyls are somewhat intermediate between these two types). Less distinction between animals of similar dietary types, but with different digestive physiology, is seen if the volumes of a single molar are compared, as suggested by Webb (1983). For example, M_3 volume for the zebra (21.02 cc) is comparable to that of the wildebeest (20.72 cc) (Table 5). This method clearly has its advantages and disadvantages. Ruminants and hindgut fermenters may be easily identified as animals of similar dietary types, despite the difference in daily ingestion of food between the two. Yet information is lost. The possibility remains that a comparison of total postcanine tooth volume in fossil ungulate taxa may serve to distinguish between types of digestive physiology in lineages that have no living representatives (for example the South American ungulate orders). Clearly, it is necessary to examine both tooth crown height, individual molar volume and total postcanine tooth volume in extinct ungulate taxa in order to determine their dietary behaviour. Table 5 provides this information for a wide variety of living ungulate species.

It seems that it is total lifetime food requirement, modified by food abrasiveness, that determines the tooth volume required of an ungulate. Animals that eat abrasive food, but which do not have the capacity for a large daily intake, would be expected to increase the tooth volume by increasing tooth crown height, since volumetric changes achieved by area changes would not limit the abrasion of the teeth. However, animals with a large daily food intake, regardless of abrasiveness, would need to increase tooth volume at least in part by an increase in tooth area, in order to increase the amount of food processed per day. Because of differences in digestive physiology, foregut fermenters would fall into the former category, and hindgut fermenters into the latter category (Janis, 1976), and it is certainly the case that hindgut fermenters have larger and more molarized premolars than do ruminant artiodactyls. Equids, which have both a highly abrasive diet, and a large daily intake as hindgut fermenters, show values for both total postcanine tooth volume and hypsodonty that are significantly greater than other ungulates. However, elephants are hindgut fermenters, yet appear to achieve their very large total tooth volume more by an increase in total tooth area than in tooth crown height. However, the unique sequential mode of tooth replacement in elephants makes it difficult to compare them directly with other ungulates.

Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Mean hypsodonty index for each diet type. Means are from data in Table 5. A, All taxa. B, All taxa minus equids, hyracoids, probocideans, and browsers in the bovid tribes Cephalophini and Neotragini. All means followed by the same letter are not significantly different from each other ($P > 0.05$) by Tukeys's Studentized Range Test.

A. ALL TAXA

DIET TYPE	N	MEAN + S.E.	RANGE	
GRAZERS (G)	19	5.18 + 0.33	1.7-8.7	A
MIXED-OPEN HABITAT (M)	42	3.80 + 0.13	1.5-5.3	B
FRESH GRASS GRAZERS (F)	8	3.20 + 0.26	1.9-4.1	B-C
SELECTIVE BROWSERS (S)	9	2.06 + 0.27	1.2-3.5	D-C
MIXED-CLOSED HABITATS (W)	21	2.05 + 0.11	1.1-3.0	D
REGULAR BROWSERS (B)	15	1.68 + 0.09	1.2-2.3	D
HIGH LEVEL BROWSERS (H)	8	1.31 + 0.16	0.8-2.2	D
OMNIVORES (O)	6	1.16 + 0.06	1.0-1.3	D

B. NO EQUIDS, HYRACOIDS, PROBOSCIDEANS, OR BROWSERS FROM BOVID TRIBES CEPHALOPHINI AND NEOTRAGINI.

DIET TYPE	N	MEAN + S.E.	RANGE	
GRAZERS (G)	11	4.78 + 0.21	3.8-6.1	A
MIXED-OPEN HABITAT (M)	40	3.89 + 0.12	2.5-5.3	B
FRESH GRASS GRAZERS (F)	8	3.20 + 0.26	1.9-4.1	B
MIXED-CLOSED HABITATS (W)	21	2.05 + 0.11	1.1-3.0	C
REGULAR BROWSERS (B)	13	1.65 + 0.09	1.2-2.3	C-D
SELECTIVE BROWSERS (S)	3	1.50 + 0.08	1.3-1.7	C-D
HIGH LEVEL BROWSERS (H)	7	1.28 + 0.18	0.8-2.2	C-D
OMNIVORES (O)	6	1.16 + 0.06	1.0-1.3	D

TABLE 2. Matrix of significance of differences between pairs of residuals, plotted from the regression line for artiodactyls and non-equid perissodactyls, of log. total postcanine tooth volume against log. body weight. Dietary abbreviations as for Table 1.

	G	F	M	W	B	S	H	O	Mean residuals:
G	0.01	-	0.001	0.01	0.01	0.01	0.01	0.05	G = 0.31
F		0.05	-	-	-	-	-	-	F = -0.07
M			0.001	0.01	0.05	0.01	-		M = -0.19
W				-	-	-	-		W = -0.18
B					-	-	-		B = -0.12
S					-		-	-	S = -0.18
H								-	H = -0.05
O									O = -0.05

TABLE 3. Matrix of significance of differences between pairs of residuals, plotted from the regression line for artiodactyls and non-equid perissodactyls, of log. third lower molar height against log. body weight. Dietary abbreviations as for Table 1.

	G	F	M	W	B	S	H	O	Mean residuals:
G	0.01	-	0.0001	0.001	0.01	0.01	0.01	0.01	G = 0.07
F		0.01	0.01	0.01	0.05	0.01	0.01	F = 0.09	
M			0.0001	0.0001	0.001	0.0001	0.001	M = 0.31	
W				-	-	0.01	0.01	W = -0.21	
B					-	0.05	-	B = -0.30	
S						0.05	-	S = -0.24	
H							-	H = -0.66	
O								O = -0.49	

TABLE 4. Matrix of significance of differences between pairs of residuals, plotted from the regression line for artiodactyls and non-equid perissodactyls, of log. third lower molar volume against log. body weight. Dietary abbreviations as for Table 1.

	G	F	M	W	B	S	H	O	Mean residuals:
G	0.01	-	0.0001	0.001	0.01	0.01	-	G = 0.36	
F		0.05	-	-	-	0.01	-	F = -1.10	
M			0.0001	0.001	0.001	0.001	-	M = 0.28	
W				-	-	0.05	-	W = -0.23	
B					-	0.05	-	B = -0.29	
S						-	-	S = -0.32	
H							-	H = -0.73	
O								O = -0.01	

Source : MNHN, Paris

TABLE 5.

SPECIES	NO. OF OBS.		TOTAL TOOTH VOLUME		HEIGHT MEASURES			B.W. (kg.)	DIET
	Area	Ht.	Mean	Range	H.I.[1]	M3 Ht.	M3 Vol.		
ORDER ARTIODACTYLA									
Family Antilocapridae									
Antilocapra americana	11	1*	16.04	13.22-19.23	4.61	3.64	6.52	50	M
Family Bovidae									
Alcelaphini									
Aepyceros melampus	9	2	14.99	12.54-18.31	4.89	3.52	5.95	53	M
Alcephalus buselaphus	16	1	32.17	26.94-41.02	5.23	4.60	10.58	136	G
Connochaetes gnou	5	1*	38.98	34.05-45.56	4.75	4.85	14.21	136	G
Connochaetes taurinus	18	1	49.08	35.90-64.33	4.94	5.63	20.72	216	G
Damaliscus dorcas	10	1	21.59	14.95-27.73	4.76	3.90	7.22	69	G
Damaliscus hunteri	7	1	26.17	22.78-29.30	4.14	4.02	10.81	88	M
Damaliscus lunatus	10	1	37.55	27.17-38.60	5.10	4.60	15.59	150	G
Boselaphini									
Boselaphus tragocamelus	9	1	35.37	23.92-43.83	3.03	3.70	13.99	210	W
Tetraceros quadricornis	7	2	3.77	2.66-4.93	2.89	2.89	1.50	17	W
Bovini									
Bison bison	9	1	120.56	95.31-138.79	4.87	7.30	46.65	675	G
Bison bonasus	1*	1*	91.01	0	6.12	7.28	32.54	625	G
Bos gaurus	6	1	101.98	87.06-111.60	3.69	6.20	41.04	755	M
Bos indicus	2	1	73.05	57.71-88.28	4.43	5.71	27.29	600	M
Syncerus caffer	10	1	77.56	50.50-99.44	3.00	4.77	29.48	620	M
Caprini									
Ammotragus lervia	5	1	23.39	20.36-26.62	4.45	3.88	9.23	86	M
Capra ibex	7	2	18.33	12.52-23.09	4.71	4.71	4.00	87	M
Hemitragus jehmlahicus	5	1	18.96	13.80-23.21	4.95	4.11	8.22	91	M
Ovis canadensis nelsoni	4	1	21.68	19.30-24.89	4.11	3.82	9.40	59	M
Pseudois nayaur	1	1	14.34	13.68-15.98	5.30	4.08	6.73	59	M
Cephalophini									
Cephalophus dorsalis	4	1	4.55	4.18-5.02	1.15	1.30	1.44	20	S
Cephalophus monticola	8	1	0.91	0.72-1.15	1.90	0.80	0.30	5.5	S
Cephalophus silviculitor	9	1	14.93	11.82-17.70	2.23	2.32	5.41	61	B
Cephalophus spadix	4	1	5.38	4.90-5.94	1.95	1.48	1.88	57	S
Silvicapra grimmia	2	2	4.42	4.11-4.79	2.97	1.72	1.46	13	B
Gazellini									
Ammodorcas clarkei	3	2	2.64	2.29-2.97	2.23	1.25	1.08	28	H
Antilope cervicapra	4	1	11.53	8.39-13.49	5.14	3.65	5.07	37	M
Antidorcas marsupialis	11	1	10.33	8.83-13.54	4.89	3.18	4.45	31	M
Gazella dorcas	7	3	4.05	2.77-5.24	3.62	1.88	1.56	23	M
Gazella granti	7	2	11.69	10.02-15.09	3.45	2.83	5.55	62	M
Gazella thomsoni	21	1	9.28	4.75-8.43	3.77	2.26	2.46	20	M
Litocranius walleri (X)	15	3	1.79	1.35-2.27	1.32	0.78	0.66	43	H
Procapra gutterosa	6	2	9.90	6.14-12.33	3.90	2.89	4.74	18	M
Hippotragini									
Addax nasomaculatis	4	1	28.48	24.59-34.93	4.09	4.17	13.80	111	M
Hippotragus equinus	9	2	36.32	38.07-57.73	4.28	4.41	12.97	270	G
Hippotragus niger	10	2	35.84	29.70-45.16	3.77	3.87	11.38	225	G
Oryx gazella	6	2	45.63	37.36-53.56	3.37	4.08	16.61	170	M
Neotragini									
Dorcatragus megalotis	3	1	2.01	1.86-2.17	2.93	1.20	0.64	9	M
Madoqua kirki	3	1	1.19	1.04-1.33	2.63	1.00	0.33	4.5	S
Neotragus pygmaeus	6	2	0.79	0.62-0.96	2.94	1.06	0.38	3.5	S
Neotragus moschatus	7	1	1.18	1.01-1.47	3.51	1.30	0.48	4.5	S
Oreibia oreibi	10	2	4.26	3.42-5.22	3.80	2.05	1.72	18	M
Oreotragus oreotragus	4	2	2.98	2.30-3.69	3.82	1.68	1.03	13.5	M
Raphicerus campestris	16	2	1.95	1.11-2.47	3.44	1.48	0.78	13.5	M
Raphicerus melanotis	8	2	1.73	1.27-2.15	2.64	1.11	0.59	10	M
Reduncini									
Kobus ellipsiprymnus	11	1	30.92	22.70-39.38	3.47	3.82	11.92	205	F
Kobus kob	2	1	11.60	10.33-13.20	3.72	2.75	3.39	57.8	F
Kobus leche	4	1	13.95	11.73-16.70	3.63	2.90	5.10	87	F
Kobus vardoni	4	2	12.93	11.18-15.03	4.05	3.04	5.05	87	F
Pelea capreolus	5	1	6.81	5.27-8.00	4.01	2.67	3.34	32	M
Redunca arundinum	9	3	9.96	7.55-13.72	3.59	2.69	4.17	62	F
Redunca fulvorufula	14	2	7.97	5.75-13.84	3.79	2.77	3.38	31	M

1. Hypsodonty Index.

Source : MNHN, Paris

TABLE 5 (cont'd).

SPECIES	NO. OF OBS.		TOTAL TOOTH VOLUME		HEIGHT MEASURES			B.W. (KG.)	DIET
	Area	Ht.	Mean	Range	H.I.	M3 Ht.	M3 Vol.		
Rupicaprini									
Budorcas taxicolor	6	1	47.05	39.33-55.40	3.43	4.43	19.23	250	M
Capricornis sumatrensis	7	2	21.69	15.57-24.91	3.93	3.73	9.14	102	M
Nemorhaedus goral	7	2	10.76	9.01-12.30	4.03	2.90	3.83	27	M
Oreamus americanus	8	1	11.25	9.52-13.19	2.76	2.35	4.98	97	M
Oribos moschatus	1*	1*	61.42	0	3.69	4.50	23.04	364	M
Pantholops hodgsoni	1*	1*	8.63	8.28-9.02	4.56	3.10	4.28	50	M
Rupicapra rupicapra	5	2	6.22	5.31-7.47	4.19	2.47	2.37	39	M
Saiga tatarica	5	2	10.70	9.74-11.73	5.29	3.28	4.69	45	M
Tragelaphini									
Taurotragus oryx	10	1	63.84	41.72-95.97	2.91	4.43	27.64	511	M
Tragelaphus angasi	12	1	12.26	9.34-15.61	2.52	2.34	5.36	91	W
Tragelaphus buxtoni	2	1	22.26	21.24-23.22	1.95	2.48	8.88	183	W
Tragelaphus euryceros	6	1	28.68	25.04-31.75	1.92	2.49	11.03	205	B
Tragelaphus imberbis	7	1	12.24	9.44-14.46	1.97	1.91	4.99	77	W
Tragelaphus scriptus	12	1	5.06	3.75-6.16	2.54	1.73	2.21	58	W
Tragelaphus spekei	4	2	9.53	8.47-10.36	2.90	2.29	3.73	74	F
Tragelaphus strepsiceros	12	1	35.55	23.67-43.83	2.29	3.07	13.60	215	B
Family Camelidae									
Camelus bactrianus	3	2	133.30	116.17-157.43	2.98	5.87	62.93	550	M
Camelus dromedarius	4	1	125.67	103.22-145.80	2.52	5.25	58.50	550	M
Lama guanicoe	4	1	20.80	17.37-24.36	3.46	3.42	8.89	110	M
Vicugna vicugna	9	2	13.50	8.73-12.95	4.33	3.55	6.67	50	M
Family Cervidae									
Alces alces (X)	7	3	66.55	53.91-80.35	1.34	2.48	18.75	384	H
Axis porcinus	4	1	7.38	7.12-7.77	2.53	1.85	2.94	42	M
Blastocerus dichotomus (X)	8	2	10.06	7.88-12.05	1.49	1.52	3.39	130	W
Capreolus capreolus	5	1	6.96	6.26-7.62	1.49	1.56	2.47	30	W
Cervus canadensis (X)	9	1	39.69	31.04-48.25	1.96	2.76	13.33	325	W
Cervus elaphus scottius	8	1	17.01	12.77-20.21	2.11	2.17	5.75	153	W
Cervus nippon	7	1	9.06	7.82-10.81	2.79	2.18	3.29	53	W
Cervus unicolor equinus	2	1	29.68	24.98-34.36	2.20	2.75	10.45	188	W
Dama dama	4	2	9.80	7.43-11.72	2.01	1.85	3.65	55	W
Elaphodus cephalophus	6	2	3.85	3.25-4.48	1.69	1.23	1.39	18	W
Elaphurus davidianus	11	1	36.78	30.81-45.40	2.35	2.84	10.65	175	F
Hippocamelus bisculus	6	4	8.63	6.19-10.43	1.94	1.61	2.85	50	W
Hydropotes inermis (X)	7	2	2.56	2.26-2.94	1.84	1.05	0.79	11	W
Mazama mazama americana (X)	5	2	3.23	2.43-3.79	1.30	0.90	0.92	20	B
Moschus moschiferus	7	2	1.71	0.84-2.17	1.98	0.97	0.56	12	W
Muntiacus muntjak vaginalis	6	2	4.66	3.58-5.82	1.81	1.34	1.61	25	W
Muntiacus reevesi	2	2	2.55	2.22-2.78	1.12	0.84	0.91	13	W
Odocoileus hemionus (X)	7	3	9.66	8.18-11.51	1.59	1.17	2.96	74	B
Odocoileus virginianus (X)	16	3	6.43	5.05-8.67	1.23	1.17	2.01	52	B
Ozotoceros bezoarticus	3	3	7.02	5.20-8.78	2.12	1.61	2.50	37	M
Pudu mephistopheles	3	1	1.53	1.42-1.61	1.61	0.90	0.52	7	B
Pudu pudu	5	2	1.96	1.57-2.69	1.62	1.00	0.66	9	B
Rangifer tarandus (X)	5	1	12.33	10.66-14.29	1.52	1.40	2.70	145	B
Family Giraffidae									
Giraffa camelopardalis (X)	25	2	60.91	43.63-75.66	1.20	2.26	16.61	1075	H
Okapia johnstoni (X)	5	4	33.86	28.52-39.18	1.18	1.96	10.70	250	H
Family Hippopotamidae									
Choeropsis liberiensis	2	1	35.05	25.33-44.62	1.37	2.28	12.93	240	B
Hippopotamus amphibius	5	1	367.72	308.87-422.14	1.91	6.38	146.48	3200	F
Family Suidae									
Babyrussa babyrussa (X)	7	2	6.37	4.89-8.35	1.03	1.11	2.70	85	O

Source : MNHN, Paris

TABLE 5 (cont'd).

SPECIES	NO. OF OBS. Area	Ht.	TOTAL TOOTH VOLUME Mean	Range	HEIGHT MEASURES H.I.	M3 Ht.	M3 Vol.	B.W. (kg.)	DIET
Hylochoerus meinertzhageni (X)	6	4	21.44	15.63-31.41	1.36	2.10	12.24	235	B
Phacochoerus aethiopicus	4	1	31.66	21.33-38.02	3.99	4.96	24.25	100	G
Potamochoerus porcus (X)	5	1	12.85	11.35-14.24	1.34	1.62	5.41	103	O
Sus scrofa cristatus (X)	6	1	16.22	12.30-20.01	1.28	1.70	9.00	120	D
Family Tayassuidae									
Catagonus wagneri (X)	1*	1*	14.53	0	1.06	1.40	4.84	38	D
Tayassu pecari (X)	4	1	8.44	7.49-9.52	1.23	1.23	2.92	32	O
Tayassu tajacu (X)	4	1	5.09	4.62-5.42	1.00	0.97	1.70	22	O
Family Tragulidae									
Hyaemoschus aquaticus (X)	6	2	1.96	1.36-2.13	1.30	0.74	0.56	12.5	S
Tragulus javanicus (X)	5	5	0.62	0.34-0.64	1.47	0.53	0.18	2.5	S
Tragulus memmina (X)	4	4	0.77	0.60-0.96	1.72	0.67	0.28	7	S
ORDER PERISSODACTYLA									
Family Equidae									
Equus asinus	4	2	115.48	99.27-133.55	8.73	6.90	15.95	220	G
Equus burchelli	23	1	111.92	86.43-155.76	5.83	6.76	21.02	235	G
Equus grevyi	6	1	171.86	142.77-197.77	5.80	7.90	32.23	400	G
Equus hemionus	5	1	159.02	141.43-177.42	5.79	7.47	25.92	290	G
Equus kiang	5	1	172.37	149.79-192.37	6.08	7.90	28.36	300	G
Equus przewalski	2	1	207.18	200.48-213.79	5.70	7.64	30.87	350	G
Equus zebra	9	2	171.88	133.67-213.42	7.06	8.75	30.80	260	G
Family Rhinocerotidae									
Ceratotherium simum	6	2	535.21	404.12-758.39	3.90	10.14	151.09	3000	G
Dicerorhinus sumatrensis	2	1	149.42	142.15-157.93	1.67	3.27	26.88	800	B
Diceros bicornis	8	2	250.38	203.23-312.97	2.24	5.05	54.79	1800	B
Rhinoceros sondaicus	2	2	193.21	157.05-220.42	1.72	4.20	43.60	1400	B
Rhinoceros unicornis	4	3	226.92	179.73-276.86	1.59	4.12	56.11	220	W
Family Tapiridae									
Tapirus indicus (X)	2	1	41.81	38.30-41.86	0.76	1.60	9.65	275	H
Tapirus terrestris (X)	5	2	28.84	25.05-34.10	0.92	1.64	7.220	240	H
ORDER HYRACOIDEA									
Dendrohyrax dorsalis (X)	8	2	0.55	0.41-0.78	1.53	0.55	0.12	4.50	H
Heterohyrax johnstoni (X)	8	2	0.37	0.31-0.42	1.52	0.47	0.09	3	M
Procavia capensis	4	2	0.67	0.42-0.91	1.69	0.61	0.17	4	G
ORDER PRDBOSCIDEA									
Loxodonta africana	—	—	7610	—	2.50	20.00	4160.00	6000	M

KEY TO DIETARY SYMBOLS (see text for further explanation):
"G" = dry grass grazer; "F" = fresh grass grazer; "M" = mixed feeder in open habitat; "W" = mixed feeder in closed habitat; "B" = unspecialized browser; "S" = selective browser; "H" = high level browser; "O" = omnivore. (X) after species name indicates that dental height values were available by direct measurement (i.e., no X-ray was taken).
A star (*) by the number of observations means that only one individual specimen was used in making all the measurements (see text for explanation).
Data on *Loxodonta africana* complied from Laws (1966) by Dr. Louise Roth.

Source : MNHN, Paris

Source : MNHN, Paris

A Quantitative Study of Australopithecine Dental Attrition

P. SMITH

ABSTRACT

Crown height, occlusal attrition scores and the bucco-lingual pitch of attrition were examined in *A. afarensis*, *A. africanus* and *A. robustus*. Crown height in all molars and the second premolars was greatest in *A. robustus*, while crown height in first premolars and canines was greatest in *A. afarensis*. In *A. afarensis* and *A. africanus*, the occlusal bevel measured bucco-lingually changed with increasing attrition, so that buccal cusp height was less than lingual cusp height (B < L). However, for similar stages of attrition, the bevel was steeper in *A. afarensis* than in *A. africanus*, producing a pongid-like occlusal plane in all cheek teeth. In *A. robustus*, a unique attrition pattern was found, a reverse bevel developed in the first molar and premolars, with B > L in the lower teeth.

These results show that the pongid-like dentofacial characteristics described for *A. afarensis* are expressed in chewing patterns. However, while attrition patterns in *A. africanus* differ from those of *A. afarensis*, they show no resemblance to chewing patterns found in *A. robustus*, and do not support hypotheses put forward of *robustus*-like dentofacial adaptations in this species.

RÉSUMÉ

La hauteur de la couronne, les stries d'attrition occlusale et l'angle bucco-lingual d'attrition ont été examinés chez *A. afarensis*, *A. africanus* et *A. robustus*. Sur toutes les molaires et les secondes prémolaires, la hauteur de la couronne atteint son maximum chez *A. robustus*, tandis que celle des premières prémolaires et des canines est plus forte chez *A. afarensis*. Chez *A. afarensis* et *A. africanus* l'angle occlusal mesuré bucco-linguale ment change avec l'aceroissement d'attrition, de sorte que la hauteur du tubercule buccal est moindre que celle du tubercule lingual (B < L). Cependant, pour des stades voisins d'attrition, l'angle est plus aigu chez *A. afarensis* que chez *A. africanus*, ce qui produit un plan occlusal de type pongide sur toutes les dents jugales. Chez *A. robustus*, on a observé un dessin d'attrition tout à fait spécial, en ce sens qu'un angle inversé s'est développé sur la première molaire et les prémolaires, avec B > L sur les dents inférieures.

Ces résultats montrent que les caractéristiques dento-faciales de type pongidé décrites chez *A. afarensis* s'expriment dans le mode masticatoire. Cependant, tandis que les dessins d'attrition chez *A. africanus* diffèrent de ceux de *A. afarensis*, ils ne montrent aucune ressemblance avec le mode masticatoire observé chez *A. robustus*, et ne soutiennent pas les hypothèses proposées d'adaptations dento-faciales de type *robustus* dans cette espèce.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris*, (série C) **53** : 389-398.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

The australopithecine dentition has been described in great detail (Robinson, 1956; Tobias, 1967; Speber, 1974, 1975; Howell, 1969; Johanson & White, 1979; Grine, 1981; Wood *et al.*, 1983). The gracile and robust australopithecines differ markedly in the relative size of anterior to posterior teeth, and this difference suggests that the two types differed markedly in dietary adaptations.

In the two gracile species, *A. africanus* and *A. afarensis*, the cheek teeth are smaller than in the robust australopithecines, *A. robustus* and *A. boisei*. However, the incisors and canines of the gracile australopithecines are larger than those of the robust species. While *A. boisei* is usually interpreted as a hyper-robust form of *A. robustus* with the same morphological pattern (Tobias, 1967), there is little agreement regarding the extent and significance of morphological differences between *A. afarensis* and *A. africanus*. Tobias (1983), Boaz (1983) and Skelton *et al.* (1986) consider them to form one chronolineage, leading to *Homo*. Conversely, Johanson *et al.* (1978, 1980, 1982), Johanson (1986), White *et al.* (1981) and Rak (1983, 1985) consider *A. africanus* to possess a number of specialized characteristics that would render it an unlikely candidate for an ancestor of *Homo*, and favour the interpretation that it was directly ancestral to robust australopithecines. This last hypothesis is largely based on the identification of a suite of primitive and generalized traits in *A. afarensis*, that are absent from *A. africanus*, as well as the identification of robust-like characteristics in the facial complex, jaw and tooth proportions of *A. africanus* (Rak, 1983, 1985; White *et al.*, 1981; Johanson, 1985).

The main differences between the dentition of *A. afarensis* and *A. africanus* as reported by Johanson & White (1979) and White *et al.* (1981), are the larger size of the anterior teeth relative to the small sized cheek teeth in *A. afarensis*. They reported that the canines in *A. afarensis* extend beyond the occlusal plane of the other teeth, and interdigitate instead of being opposed as in the other australopithecines and in *Homo*. They further noted that the lower first premolars in *A. afarensis* are asymmetrical, with the lingual cusp underdeveloped as in pongids. However, the metric differences between *A. afarensis* and *A. africanus* are small. Likewise, the sample sizes, especially of unworn teeth with all morphological characteristics preserved, are small, so that some researchers consider that larger samples of both types are necessary before firm conclusions can be reached.

While inferences based on dental morphology are restricted to intact teeth with little wear, the pattern of attrition can be studied on all teeth. Attrition patterns reflect functional adaptations relating to jaw relationships and chewing patterns. If the morphological differences reported between the teeth and jaws of *A. afarensis* and *A. africanus* are significant, they should affect tooth-jaw function, and so be reflected in the pattern of dental attrition. Similarly, if *A. africanus* does show *robustus*-like characteristics in the teeth and jaws, these should be reflected in a similar pattern of attrition between these two species.

The underlying assumption of studies of attrition is that the amount of attrition reflects the severity of abrasive forces acting on the teeth, while the pattern of attrition reflects the direction and extent of tooth contacts during mastication. However, the amount of attrition is also correlated with the length of time the tooth has functioned, tooth size, enamel thickness and micro-hardness. Likewise, arch form and tooth-jaw relationships modify the area of the tooth surfaces in contact during protrusion and lateral excursion. Molnar & Ward (1977), pointed out that the rate at which dentine is exposed, varies not only with the amount of frictional forces applied to the teeth, but also with the microstructure of the hard tissues, enamel thickness, crown shape and area, and direction of force applied. As shown in Fig. 1, tooth size affects the rate at which dentine is exposed, because of differences in enamel thickness between teeth. For any one population, with the exception of those affected by enamel dysplasias, the extent of morphological variation in dental structure is minor relative to the discriminatory power of scoring methods used. Given the wide range of interpopulation variability in tooth size and morphology, attrition scores alone may not provide a very accurate method of comparing dental function in groups with major differences in tooth size and/or chewing patterns.

In fossil hominids, the range of variation in tooth size and morphology is far greater than in

Source : MNHN, Paris

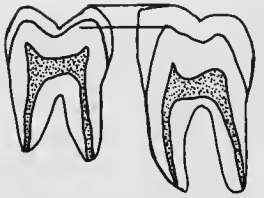

FIG. 1. — Diagram showing effect of differences in tooth size and enamel thickness on attrition rates.

Homo sapiens sapiens. Once again, this is irrelevant when assessing the severity of attrition relative to tooth mass within any one group. However, in order to compare the severity of abrasive forces between populations, some allowance should be made for differences in dental morphology. One method that takes these factors into account, compares attrition scores to crown height and occlusal slope. Assuming that increments in attrition for all cusps are proportional to enamel thickness, cusp area and angle, the regression of crown height on attrition will vary with enamel thickness, and the thicker the enamel the shallower the slope. As attrition proceeds, the bucco-lingual pitch of the occlusal plane will change if there is uneven contact over the occlusal surface. This should not affect the correlation between buccal crown height and attrition scores on the buccal cusps, unless the occlusal plane becomes markedly steep.

In this study I have utilised this method to examine attrition patterns in *A. robustus, A. africanus* and *A. afarensis*, and the implications of differences in attrition to dental function.

Material and Method

This study was carried out on the permanent teeth of Australopithecinae from the Southern African sites of Swartkrans, Kromdai, Sterkfontein, Makapansgat and Taung, held in the collections of the Department of Anatomy, University of Witwatersrand, and the Transvaal Museum, Pretoria. In addition, master casts of teeth from the Afar, Ethiopia, held in the collections of the Anthropology Department, University of California at Berkeley, were studied. While the use of casts for the *A. afarensis* specimens may reduce the reliability of measurements recorded for this species, differences between measurements taken on the casts and those taken on original specimens averaged less than 3 %. In all, 234 teeth attributed to *A. robustus*, 151 teeth attributed to *A. africanus* and 113 teeth attributed to *A. afarensis* were studied.

For each tooth the anatomical crown height was measured on the buccal surface along a line parallel to its main axis. All teeth were measured from the cemento-enamel junction. The incisors and canines were measured to the incisal edge, the premolar to the tip of the buccal cusp, and the molars measured to the tip of the mesiobuccal cusp. A six point attrition scale was used (Smith, 1972) where 1 = no attrition; 2 = attrition of enamel facets more than 1 mm in diameter; 3 = dentine exposed on cusp tips; 4 = cupping of dentine; 5 = secondary dentine exposure; 6 = pulp exposure or wear to the root. Attrition was scored for the occlusal surface of the incisors and canines. The buccal and lingual cusps of the premolars were scored separately and so were each of the main molar cusps (MB mesiobuccal; ML mesiolingual; DB distobuccal; DL distolingual). From these data, mean crown height, attrition scores and correlation coefficients between crown height and attrition were calculated, and least mean squares regression lines plotted, using SPSS programmes (Nie *et al.*, 1975). Finally the occlusal pitch of teeth was scored by placing a scale perpendicular to the crown-root axis of each tooth and recording the buccolingual pitch, where 1 = buccal cusp higher than lingual (B > L), 2 = (B = L) and 3 = (B > L).

Results

Fig. 2 and Fig. 3 demonstrate the range of values recorded for crown height of teeth in the three species studied. The premolars are listed here as P1 and P2, using the nomenclature commonly used for the hominid dentition. (This

Source : MNHN, Paris

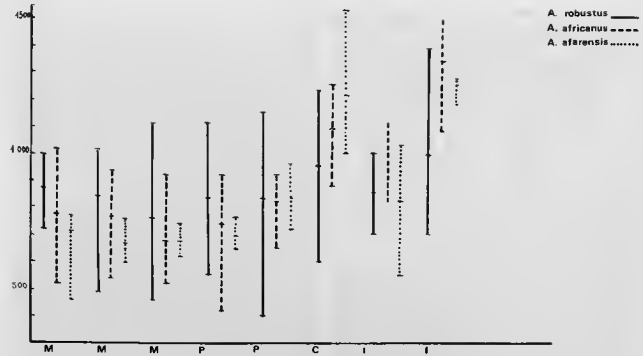

FIG. 2. — Crown height of maxillary teeth.

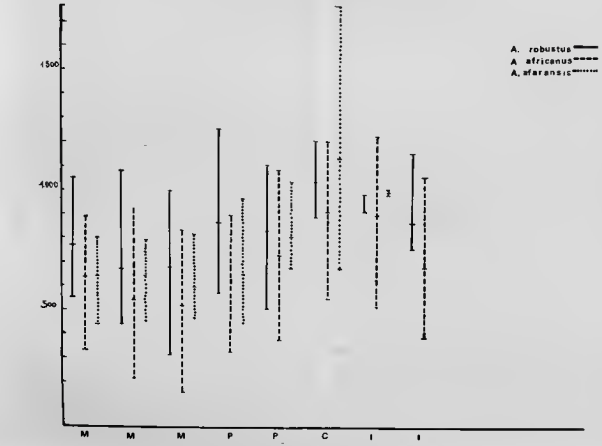

FIG. 3. — Crown height of mandibular teeth.

Source : MNHN, Paris

is not a statement regarding the phylogeny of these teeth, which are generally recognized as the third and fourth of the four premolars present in ancestral mammals). The maximum values recorded for crown height may be considered representative of unworn crown height, while the mean and minimum values give an estimate of the extent of attrition that has occurred. The number of specimens examined, and mean attrition scores, are shown in Table 1. Since most of these values were derived from isolated teeth, they cannot be used to reconstruct the pattern of attrition along the tooth row. Unworn crown height, as defined here, was greatest in *A. robustus* for premolars and molars, while canine crown height was greatest in *A. afarensis*. Crown height in *A. africanus* upper and lower canines and upper second and third molars closely resembled that of *A. robustus*, while crown height measurements of most other *A. africanus* teeth were closer to those of *A. afarensis*. Though mean attrition scores in all upper molars were greatest in *A. robustus*, mean crown height was still greatest in this species. For teeth from the lower jaw, the most severe attrition was found in *A. africanus*.

Tables 2 and 3 show the frequency distribution of teeth with an occlusal pitch such that the buccal cusps are lower than lingual cusps (B < L) in the lower teeth. Since this could not be accurately scored in all teeth, sample sizes given differ somewhat from those of Table 1. Data are given both for teeth with minimum attrition (grades 1 through 3) and moderate to severe attrition (grades 4 to 6). The buccolingual pitch of the lower molar teeth differed in all three species studied. In *A. africanus* and *A. afarensis*, the percentage of individuals with B < L increased in premolars and first and second molars, as attrition increased in severity. However, in *A. afarensis* the frequency of teeth with B < L was much higher for both groups of attrition. In the third molar of both species the occlusal plane was B< L, even in severely worn third molars of *A. africanus*. None of the *A. afarensis* third molars were severely worn and all attrition grades were below 4.

In *A. robustus*, there was a lower percentage of individuals with B < L than in either of the gracile australopithecines. In the first molar and premolars a reverse pitch developed as attrition proceeded, as the lingual cusps were worn more rapidly than the buccal cusps, such that B > L. This reverse pitch was also found in the lower anterior teeth, especially canines, of specimens from Swartkrans with severe attrition.

The correlation coefficient of crown height with attrition was high, ranging between r = -0.9 to r = -0.4, for all teeth other than M3 in *A. afarensis* (Table 3). The regression line calculated from the least mean squares distance is shown in Fig. 4. In *A. robustus*, the slope was shallowest in

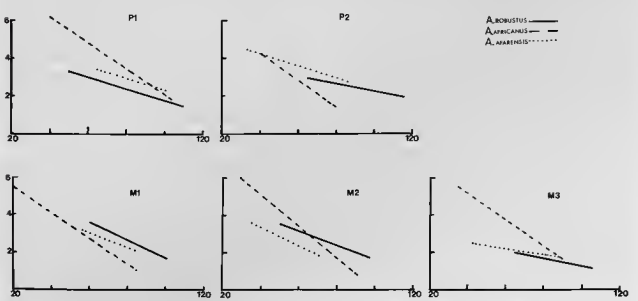

FIG. 4. — Regression of crown height on attrition.

Source : MNHN, Paris

the premolars, intermediate in the third molar, and steepest in the first molar. In *A. africanus* the slope was steepest in the second molar. In *A. afarensis*, the slope was flattest in the premolars, intermediate in the third molar and steepest in the first molar. Of the three species, *A. africanus* showed the steepest slope followed by *A. afarensis*, with a very similar pattern in the first and second molars. Comparison of the three species shows that, in the cheek teeth, the shallowest slope of attrition on crown height was found in *A. robustus*. That is, for every increment of attrition in the cheek teeth, there was a greater reduction in crown height in *A. robustus*, than in *A. africanus*.

Discussion

Of the three species studied here, *A. robustus* has the thickest enamel (Robinson, 1956; Grine, 1981; Sperber, 1985) and the smallest mesial cusps, relative to the gracile australopithecines (Sperber, 1974; Wood, 1981; Wood *et al.*, 1983). The regression of crown height on attrition reflects these differences in enamel thickness and occlusal pitch. For every increment in attrition, there was more tooth material lost in *A. robustus* than in the other two species, as would be expected due to its thicker enamel.

Even when taking into consideration the differences in enamel thickness, the pattern of attrition in *A. robustus* is unique. The data obtained for the occlusal pitch indicate that even in the early stages of attrition there is an occlusal slope with B < L in 25 % of third molars, indicative of a buccal tilt to this tooth. With further attrition the frequency of *A. robustus* specimens with an occlusal slope of B > L increases in the lower first molar region as attrition progresses. This is the reverse trend to that observed in *A. africanus*, *A. afarensis* or *Homo*, and is indicative of a reversed relation of upper and lower tooth contacts in this region. These findings agree well with those of Robinson (1956) and Wallace (1975, 1978) for robust australopithecine attrition. They reported large numbers of premolars and anterior teeth, in both jaws, with moderate and severe attrition showing reverse bevel of the occlusal slope. It is also in accord with the results of SEM studies showing differences in direction as well as depth and breadth of scratches on facetted areas between *A. robustus* and *A. africanus* (Grine, 1981 and Walker, 1981).

The results of this study confirm that in *A. robustus* a functional crossbite extended as far posteriorly as the mesial cusps of the first molars. This may be partially due to differences in arch relationship, with the lower jaw wider than the upper in *A. robustus* as suggested by Robinson (1956) or related to a retruded maxilla and extensive protrusive movements of the mandible in mastication.

In all three molars of both *A. africanus* and *A. afarensis*, the frequency of occlusal pitch of B < L increased as the severity of attrition increased, though at a different rate. While the sample sizes studied here are small, they suggest that a B < L occlusal bevel was present at an earlier stage of attrition in *A. afarensis*, and that the pattern of attrition in all three molars was more similar than in *A. africanus*. This pattern of attrition resembles that recorded in non-human primates (Welsch, 1967; Smith, 1969; Gantt, 1979; Teaford, 1983). It may be related to the form of the dental arches and canine size. Primitive features described in the teeth and jaws of *A. afarensis* include: distal rather than occlusal facets of attrition, parallel tooth rows, asymmetric, first premolars and fenestration of the buccal cortical plate of upper premolars (Ward *et al.*, 1982; Johanson *et al.*, 1982). The mandibular corpus also displays a number of features in common with those of apes (White *et al.*, 1981).

While attrition patterns in *A. africanus* differ from *A. afarensis*, they also differ from those observed in *A. robustus*. They are the most *Homo* like of the three species studied, and do not support hypotheses that propose a *robustus*-like, functional pre-adaptation in the face and jaws of *A. africanus*.

None of the australopithecines studied here showed any tendency towards the development of a helicoidal plane at any stage of attrition. These results do not support Osborne's (1982) proposal that the absence of a helicoidal plane in the australopithecines was related to the particular stage of attrition present. In *Homo sapiens* with normal occlusion, that is, a maxillary overjet, the lower teeth tilt lingually, and the upper teeth tilt bucally when they erupt. As a result, the

Source : MNHN, Paris

lower buccal and upper lingual cusps make contact first and wear more rapidly than the other cusps, except in the third molar region where the overjet is minimal or even reversed. This means that in the lower third molar either all cusps are worn equally, or that the lingual cusps are worn most, maintaining an occlusal pitch such that B > L. This has been reported for a wide range of both fossil and recent populations by Campbell (1925), Ackerman (1953), Murphy (1959, 1964), Butler (1972), Hall (1976) and Brown *et al.* (1977). Tobias (1980) considered the lack of a helicoidal plane in *A. robustus* and *A. africanus*, as due to the more parallel jaws of these species, as compared to the horseshoe-shaped, upper dental arch in *Homo*. Holly Smith (1986) reported that the angle of implantation of the teeth, rather than arch relationships, may determine the formation of the helicoidal plane. However, for proper intercuspation of opposing molars, it is arch relationship that determines the direction and tilting of teeth. In an earlier study of human skeletal remains of populations with different dietary adaptations, Holly Smith (1984) reported that diet was the main variable affecting occlusal pitch. This, presumably because of differences in the direction and intensity of chewing patterns needed to masticate foods of varied composition.

Although Campbell (1925), and Murphy (1959, 1964), found that in Australian Aborigines the helicoidal pattern developed with more severe attrition, Kieser *et al.* (1985) reported that the occlusal plane changed from B > L to B < L, in 17 % of the lower third molars of South American Lengua Indians. This study is one of the few carried out on a living population, with good control for sample sizes in different age groups. The shift from B > L to B < L occurred as attrition increased in severity, with dentine exposed on all cusps, demonstrating that the helicoidal plane does not invariably develop even in recent human populations.

This study has demonstrated differences in attrition patterns between the three australopithecine species examined: *A. robustus*, *A. africanus* and *A. afarensis*. The consistent development of a reverse bevel of occlusal attrition in *A. robustus*, suggests that the mandible in this species is functionally prognathic, relative to the very retruded maxilla. This feature is not found in either *A. afarensis* or *A. africanus*. However, while both *A. afarensis* and *A. africanus* show attrition patterns consistent with a maxillary overjet and lack of narrowing of the maxilla posteriorly, *A. afarensis* develops a steep B < L occlusal pitch in all three molars that is characteristic of attrition patterns of the cercopithecoids and pongids. This may be related to the role of the canines in limiting protrusion (Smith, 1969), although this has been questioned by Gantt (1979). The occlusal pitch in *A. africanus* is flatter, and more comparable with that observed in *Homo*, but differs in the third molar region. None of the species studied here developed a helicoidal occlusal plane at any stage of attrition.

The method adopted in this study, provides a simple, easily duplicated and reliable method for quantifying attrition patterns in relation to tooth size. It further permits the assessment of the severity and direction of attrition, and may prove of value in species assignation of isolated and/or abraded fossil teeth.

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Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Mean attrition score for specimens listed in Fig. 2.

Tooth	*A. robustus*		*A. africanus*		*A. afarensis*	
MAXILLA	No.	attrition score	No.	attrition score	No.	attrition score
M 3	13	2.2	14	2.3	3	2.0
M 2	19	3.4	16	2.8	4	2.1
M 1	26	4.0	18	3.3	5	3.1
P 2	19	3.7	15	3.0	5	2.2
P 1	17	3.5	11	3.2	5	2.1
C	11	4.4	7	2.7	3	3.7
I 2	4	3.8	4	2.7	3	3.5
I 1	9	3.8	4	2.6	2	4.0
MANDIBLE						
M 3	14	2.0	10	2.8	13	2.0
M 2	19	2.8	10	4.9	15	2.3
M 1	21	3.2	8	4.8	15	2.9
P 2	23	2.5	6	4.2	15	2.8
P 1	15	2.5	8	3.7	14	2.5
C	9	2.6	8	4.6	4	2.9
I 2	3	3.0	3	4.6	2	4.0
I 1	4	2.8	5	5.3	—	—

TABLE 2. Frequency distribution of occlusal pitch in teeth with minimal attrition.

Tooth	*A. robustus*			*A. africanus*			*A. afarensis*		
	no	% B < L	% B > L	no	% B < L	% B > L	no	% B < L	% B > L
P1	7	28	72	2	0	100	11	36	64
P2	14	7	93	5	0	100	11	54	46
M1	14	64	36	4	50	50	8	88	12
M2	17	35	65	5	20	80	12	75	25
M3	16	25	75	13	38	62	10	60	40

TABLE 3. Frequency distribution of occlusal pitch in teeth with moderate to severe attrition.

Tooth	*A. robustus*			*A. africanus*			*A. afarensis*		
	no	% B < L	% B > L	no	% B < L	% B > L	no	% B < L	% B > L
P1	1	0	100	3	33	67	2	50	50
P2	2	0	100	5	60	40	4	100	0
M1	1	33	67	8	88	12	9	100	0
M2	6	67	33	5	80	20	4	100	0
M3	—	—	—	3	67	33	—	—	—

TABLE 4. Correlation coefficients calculated between anatomical crown height and attrition scores in lower premolars and molars.

Tooth	*A. afarensis* r	*A. africanus* r	*A robustus* r
First premolar	-.5	-.91	-.54
Second premolar	-.8	-.96	-.43
First molar	-.5	-.89	-.84
Second molar	-.7	-.89	-.43
Third molar	(-.2)	-.86	-.44

Source : MNHN, Paris

Tooth Microwear in *Homo habilis* at Olduvai

P.-F. PUECH

ABSTRACT

The Olduvai *Homo habilis* fossils are the early representatives of the genus *Homo*, two million years ago. They lived side by side with another hominid species: *Australopithecus boisei*. From similar tooth wear patterns of extant species, microscopic observations reveal persuasive evidence of food choice for both *H. habilis* and *A. boisei*. The distinctive features of *H. habilis* are few abrasive alterations, fatigue and erosive wear associated with a specific incisal wear giving evidence of separation of Cyperaceae and/or Gramineae food. In contrast, *A. boisei* is characterized by fatigue and friction wear and more damaged enamel by abrasive grains. It is supposed that the roots of vegetables caused more grit to be eaten. On the incisors' labial enamel of both species we have not noticed the deep gashes which in some later hominids are related to a specific feeding adaptation.

RÉSUMÉ

Les *Homo habilis* fossiles d'Olduvai font partie des premiers représentants du genre *Homo* et datent de deux millions d'années. Ils vivaient côte-à-côte avec une autre espèce d'hominidé, *Australopithecus boisei*. Le choix alimentaire de ces hominidés peut être déduit de la comparaison des aspects de l'usure des dents avec ceux d'hommes et d'animaux actuels. Les traits distinctifs de l'usure des dents d'*Homo habilis* consistent en de rares traces d'abrasion, en une usure par fatigue et par érosion ainsi qu'en un type particulier d'usure des incisives qui témoigne de la sélection par cette espèce d'une nourriture à base de Cypéracées et/ou de Graminées. Les dents d'*Australopithecus boisei* sont caractérisées par une usure par fatigue et friction ; de plus l'émail est davantage altéré par les matières abrasives ; ces particules abrasives sont supposées provenir des racines des végétaux. L'émail labial des incisives des deux espèces ne montre pas les profondes balafres qui, chez certains hominidés plus tardifs, correspondent à une adaptation alimentaire particulière.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris*, (série C) **53** : 399-414.

Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

Introduction

The type series of specimens for the species *Homo habilis*, representing the first appearance of *Homo* two million years ago, was discovered in northern Tanzania at Olduvai (Leakey *et al.*, 1964). At Olduvai, side by side with *Homo*, also lived the hominid species *Australopithecus boisei*.

Research on variation in early hominids and on the cultural nature of hominid adaptation shows that the close affinities of the two species warrant the comprehensive studies made of their dental adaptations related to diet (Robinson, 1956; Peters, 1981; Puech *et al.*, 1983a). *Homo* developed large incisors which had a better resistance to wear and/or for more incisal preparation, as inferred from similar adaptation in frugivores (Hylander, 1975; Kay, 1977, 1984). In contrast, *A. boisei* has reduced incisor size probably to allow more room for hyper-enlarged-premolars and molars, a dental adjustement related to a savanna habitat (Jolly, 1970). However there are common adaptations in the two species, both having enlarged postcanine teeth that are covered with thick enamel.

The hypotheses of early hominid diet based on analyses of the angulation of occlusal wear facets of the cheek teeth and quantitative analyses of the features of wear are of no use in a comparative study of *Australopithecus* and *Homo* because of morphological variations in the masticatory complex. Therefore in order to discriminate possible dietary categories reflected in tooth wear, we present a microscopic analysis of the dental crowns in *H. habilis* and *A. boisei*. The purpose of this study is only to describe the specific features of wear and not to compare wear facets, so these observations will not deal with the pattern of wear itself.

Material and Method

The initial *H. habilis*, Olduvai Hominid 7 (O.H.7), includes a fragmentary skull with a juvenile mandible estimated to have been 10 years old. The second specimen, O.H.13, a partial skull with a complete dentition, has tooth crowns somewhat damaged by post-mortem erosion so that microscopic analysis is not possible. The third habiline, O.H.16, nicknamed " Olduvai George ", was severely fragmented when it was unearthed. It represents the rare early hominid with matching upper and lower dentitions. The *A. boisei* material is comprised of O.H.5 "Zinjanthropus ", recovered by Mary Leakey in 1959 (Leakey, 1959; Tobias, 1967), and the Peninj mandible from the lower parts of the Ileret sequence 50 miles north-east of Olduvai Gorge (Leakey & Leakey, 1964), two specimens falling within the Olduvai normal magnetic event (1.6-1.9 m.y.) such as O.H.7 and O.H.16 from Olduvai Bed 1 and lower part of Bed 2 (Fig. 1).

The teeth examined were carefully cleaned with acetone in order to eliminate dust particles. Then a nitrocellular impression was made with varnish that provides planar portions of curved surfaces. The choice of a nitrocellular varnish is made to allow observation by photonic transmitted light and scanning. Negative impression provides necessarily more details and less artifacts than duplication with a two step replication. Wear traces are observed under magnifications from 10 to 500 using the techniques described by Puech (1980).

Results

A. *Dental wear*

In *H. habilis* and *A. boisei* the abrasion of teeth produces smooth occlusal surfaces and provides evidence of a rapid rate of dental wear. Theoretically such wear reflects consumption of food that requires high occlusal stress. The large habiline male, O.H.16, shows exposed dentine on every tooth before the third molar erupted into occlusal position, and the lower teeth occluded mesially to their normal position with their maxillary homologues. The edge-to-edge occlusion of the front teeth seems to have been the type of occlusion in Olduvai hominids producing horizontal occlusal wear in the incisors such as present in O.H.5 (Fig. 2), O.H.7 and O.H.16. No crowding of the front teeth is evident for *H. habilis* but *A. boisei* from Peninj presents a slight crowding (Fig. 3).

The microscopic examination of the appar-

Source : MNHN, Paris

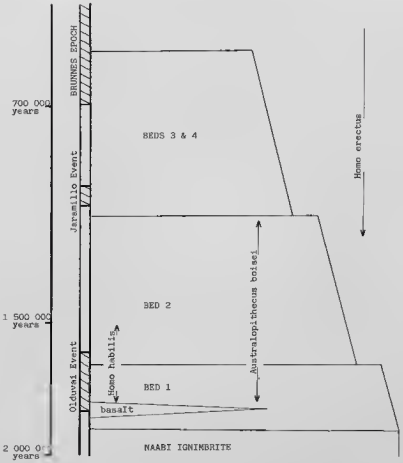

FIG. 1. — Early hominids at Olduvai Gorge (Tanzania): time scale, magnetic epochs and stratigraphic beds.

FIG. 2. — Smooth flat occlusal wear with rounded borders in *Australopithecus boisei* Olduvai Hominid 5 (Courtesy of P. V. Tobias).

Source : MNHN, Paris

FIG. 3. — *Australopithecus boisei* from Peninj presents a slight anterior dental crowding (Courtesy of P. V. Tobias).

ently smooth aspect of *H. habilis* dental surfaces, gives evidence of patinated enamel bringing the underlying structures into relief in places so that at high magnification a punch-board texture, enamel rods and Hunter-Schreger bands are apparent. Cheek teeth are poorly striated as a consequence of food containing little detritic material or having been washed (Fig. 4). Among apes, poorly striated teeth result from a lack of interest for dusty underground food (Walker, 1976). Eskimos also present fine scratches and abundant small fatigue pits. From these parallels, it is probable that the punch-board texture in *H. habilis* results from a powerful crushing.

Buccal and labial sides of the occlusal surfaces of the teeth of *H. habilis* reveal striae and grooves predominantly bucco- or labio-lingual by oriented. This wear pattern seems to result from " scraping ", " stripping " or " shearing " items. Under higher magnification, the grooves are

Source : MNHN, Paris

FIG. 4. — Negative cast of the Olduvai Hominid 7 first lower right molar occlusal surface. The distinctive features are very few abrasive alterations with an etched and patinated enamel and dentine.
B = buccal; L = lingual.

almost parallel and of approximately uniform diameter and spacing (Fig. 5). The slight elevations seem to be smoothly polished and the depressions come from chemical etching (Fig. 6). This pattern indicates a process of wear involving the combination of physical and chemical activities of vegetarian origin, since the same fabric-like " furrows " are common in animals eating herbage and swampy plants. Occlusal enamel of the cheek teeth of sheep have a " furrowed " pattern in relation with the enamel prisms arrangement. This pattern can only result from the mastication of Gramineae. These plants contain a siliceous skeleton of opal phytoliths; this amorphous silica is responsible for the parallel scratches varying in width from 0.2-1 μm in mammalian teeth (Walker *et al.*, 1978). These fine parallel scratches can be confused with scratches produced by the exogenous grit adhering to plants (Covert & Kay, 1981) but in many cases microscopic examination allows detection of the origin.

In ancient Egyptian teeth, for example, "furrows" different from scratches (Fig. 7) have been attributed to perennial plants, *Cyperus papyrus*, which grows on the marshy banks of the Nile (Puech *et al.*, 1983b). Phytoliths in the Cyperean family appear as silica situated at the bottom of cells, their apex pointing towards the exterior walls. The phytolith cone, about 8 μm thick, are rarely solitary but grouped in a cluster composed of a variable number. Ancient Egyptians ate young shoots of *Cyperus papyrus* and we suppose that early man did the same with swampy plants. Under a pressure of 10 kg, twice the amount necessary for the structural breakage of the stem of *Cyperus*, the striation produced on enamel in experimental studies is about one twentieth of the width of the abrasive particle (Puech & Prone, 1979). The striations produced by phytoliths should then be 0.4 μm wide, close to the mean value of the " scratches " produced by grass on enamel (Walker *et al.*, 1978).

The characteristics of the " furrows " are probably the result of a multiplicity of factors occurring during the mastication of plant tissues (Rensberger, 1978). An explanation of the physi-

Source : MNHN, Paris

FIG. 5. — Central upper right incisor of Olduvai Hominid 16. The occlusal surface gives evidence of a specific incisal use by labio-lingually oriented furrows and striae.
B = buccal; L = lingual.

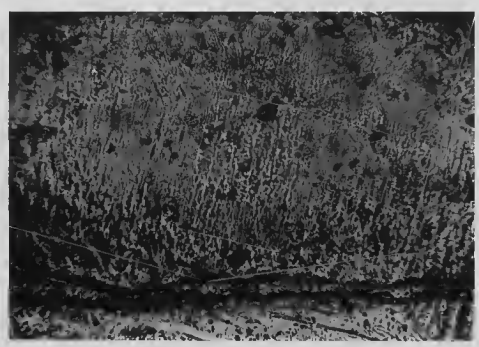

FIG. 6. — Central incisal surface of the central upper right incisor of Olduvai Hominid 16, × 50. The furrows running from the enamel-dentine junction are almost parallel and of uniform diameter and spacing.

Source : MNHN, Paris

FIG. 7. — Furrows in ancient Egyptian teeth — upper left of the figure — are attributed to a wear process involving mastication of Cyperaceae. × 50.

cal and chemical events leading to the production of " furrows " has already been proposed (Puech, in press). Based on the polishing resulting from the friction of food and on the granulometric distribution of phytolith particles, Cyperaceae and Graminae produce the characteristically blunt appearance of wear associated with fine " striae " (Fig. 8).

The erosive action of the diet of *H. habilis* from Olduvai is confirmed by a burnished appearance of the second upper molars in O.H.16. These second molars showed localised hypoplasia and erosion that were the result of chewing habits (Tobias, 1976). The same pattern of erosion has recently been noted in extant human juveniles who chew aspirin for the relief of rheumatoid arthritis (Sullivan & Kramer, 1983), and thus Puech (1984) related the burnished appearance seen in O.H.16 with the injurious effects of chewing resistant acidic material (Fig. 9).

Hypoplasia of the enamel is a common feature in Olduvai hominids. The type specimens of *A. boisei* (Fig. 10) and *H. habilis* (Fig. 11), namely O.H.5 and O.H.7, were affected. From the levels of strips of hypoplastic enamel in O.H.5, Tobias (1974) concluded that the *A. boisei* youth had

FIG. 8. — Blunt appearance of the furrows present in the lateral lower incisor of Olduvai Hominid 16, × 500. Central labial margin of the occlusal surface.

Source : MNHN, Paris

FIG. 9. — Burnished second upper right molar in Olduvai Hominid 16 and the localized erosion attributed to the chewing of resistant acidic vegetables (Courtesy of P. V. Tobias).

FIG. 10. — Hypoplasic grooves and pits on the labial enamel in Olduvai Hominid 5 (Courtesy of P. V. Tobias).

been subject to systemic upsets. Hypoplasia and acidic food acted in combination producing the concave erosion that occurs on the second molars of O.H.16. Food accumulated in the major occlusal pit, and because the enamel there was thinner and hypoplasied, the topical effect was most injurious.

In contrast, *A. boisei* fed on more dusty material that has produced smooth, flat occlusal wear with rounded borders. Microscopically, the teeth of *A. boisei* appear to have been damaged by abrasive grains; the latter moreover produced micro-pits in the incisor enamel during grasping action, and deeply striated the posterior teeth during the grinding of food (Figs. 12 and 13). Furthermore the occlusal margins of the interstitial surfaces are frequently irregular and polished, suggesting that microscopic irregularities of the surface are caused by enamel fatigue and abrasive material. Foraging habits in the Chacma baboon includes extraction of belowground vegetables; our analysis of dental microwear shows a similar abrasive grain action. In consequence, we accept the thesis of the use of an earth-digging stick as being responsible for the high percentage of abrasive particles that have worn down *A. boisei* teeth, producing smooth rounded occlusal borders and a deeply recessed dentine. Con-

Source : MNHN, Paris

FIG. 11. — Hypoplasia (central dark region) and absence of deep grooves on labial enamel of the central lower right incisor of Olduvai Hominid 7, × 50. Occlusal surface at top.

sumption of belowground plants in combination with food having a high friction action, associated with heavy mastication, seems to be responsible for hyper-enlarged cheek teeth.

In the front teeth, striations result from the movement of mandibular teeth during ingestion and mastication as well as from the use of the hands to hold, pull or push food and other objects. In *H. habilis* and *A. boisei*, incisal dentine presents large mesio-distal striae produced by a slicing action. On the labial surfaces no additional deep grooves have been observed. These grooves in monkey (*Papio ursinus*) and later hominids (*H. erectus* and *H. sapiens*) come from the common use of front teeth to assist the hands.

B. *Habitat*

The *H. habilis* and *A. boisei* remains at Olduvai and Peninj were discovered in alluvial and lacustrine sedimentary deposits interbedded with volcanic aeolian tuffs. The length of the sequence in which *H. habilis* was recovered together with *A. boisei* shows that apparently no niche divergence occurred.

The fossil Olduvai fauna (that closely resembles the extant fauna), as well as palaeobotanical information, indicate the persistence of wooded grassland and of an acacia savanna environment in early hominid-bearing sediments (Bonnefille, 1985; Denys, 1985; Jaeger, 1976, 1979; Leakey, 1965; Petter, 1973; Rage, 1973). Palaeoecological reconstruction of the way of life of early homin-

Source : MNHN, Paris

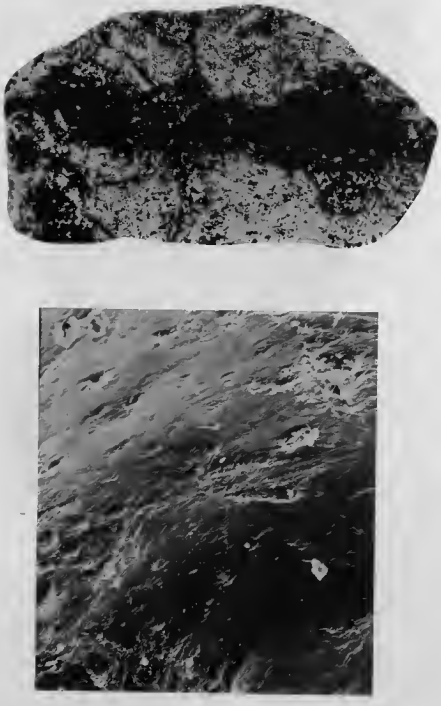

FIG. 12. — Damaged occlusal surface of a lateral lower incisor in *Australopithecus boisei* at Peninj, low (× 30) and higher (× 300) magnification. Labial surface down.

Source : MNHN, Paris

FIG. 13. — Polished occlusal enamel with many striations in the second lower left premolar of the Peninj mandibule. Striations running from buccal, at left, to lingual surface at magnification of 50.

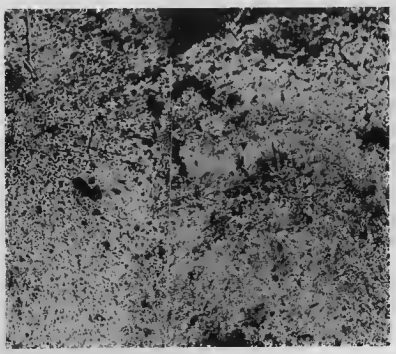

FIG. 14. — Etched occlusal enamel of the first lower right molar of Olduvai Hominid 7. Detail × 50 from Fig. 4

Source : MNHN, Paris

ids at Olduvai testify to a lake margin or flood plain setting (Hay, 1976). Swampy vegetation is indicated by vertical non-branching root casts, and marshland by identification of *Cyperus papyrus*. *Cyperus papyrus* and other *Cyperus* species have a particular nutritional richness (Hatley & Kappelman, 1980).

Savanna type habitat and lake margins are characterized by vegetable species that produce nut-like fruits, legumes, tubers, rhizomes, roots and stem bases of water-edge plants. Thus, basically, sources of vegetable food for omnivore hominids were diversified. Furthermore stone tools associated with animal bone remains imply a meat-eating habit by Olduvai *H. habilis*. Apparently the decisive factors of food choice must have been seasonal and annual availability as well as qualitative composition of the food.

Discussion and Conclusion

In monkeys the use of incisors varies according to the species, even if they process similar food. Walker (1976) presented observations giving evidence that *Papio* used incisors to process lettuce twice as much as did *Colobus*. The absence of deep grooves on the labial faces of the front teeth in *H. habilis* and *A. boisei* may, as well, not be exclusively due to the absence of special mechanical demands.

Molar microwear provides a good guide for detecting food choice since cheek teeth have the sole function of grinding food before swallowing. However no microwear feature can be exclusively attributed to bone-crushing or to scraping and slicing meat because in carnivorous mammals teeth have a polished enamel that is inconclusive for hominids (Puech, 1980). Evidence of meat eating in *Homo* is therefore to be searched for rather in detailed studies of stone artefacts and in cut-marks on bones.

On microscopic examination the molar teeth of *H. habilis* from Bed 1 and Bed 2 at Olduvai reveal evidence of enamel and dentine erosion (Figs. 14 and 16). The erosion affecting all crown surfaces and accelerating tooth wear results in a typical microscopic appearance. From this it would appear that the Olduvai habilines chose acidic food. Ripe fruits are a dietary staple for apes. In some areas, however, orang utans and chimpanzee specialize seasonally on unripe fruits (Fig. 15) (Galdikas, 1982; Nishida *et al.*, 1983) and Chacma baboons eat bitter fruits rejected by birds. Like the Chacma baboon (Hamilton *et al.*, 1978a), *H. habilis* may have selected the immature stages of most vegetation and some fruits to reduce the cellulose content and to secure fruits before other animals could feed on them.

Cyperaceae, with a particularly high mineral content in the form of phytoliths, have produced a characteristic pattern in the incisives of *H. habilis* (Fig. 17). *Cyperus* was available to *Homo* and *Australopithecus*, but Hamilton *et al.* (1978b) report that *Cyperus* root-processing observed in baboons does not occur in other animals because it needs manual dexterity to separate the protective sheaths from the bulbs and stems. Cyperaceae from swamp margins and river banks is a starchy food that could have been sufficient for the energetic needs of early man, but its consumption is a time-consuming habit only adopted in ancient Egyptians when a decline in alternative resource was occurring. Comparative microwear analyses, ethnological and palaeoecological documentation are thus providing evidence of acidic swampy vegetable feeding by *H. habilis* at Olduvai.

variety of food items and only some of these items produced the features described in the present study. It is also evident that some features are related to differences in occlusal forces that can be inferred from the morphology of the masticatory systems (Rak, 1985). However, microwear gives evidence that the two hominid species at Olduvai, *A. boisei* and *H. habilis*, had a divergent food choice. Together with a time-table concerning the occupation of water holes, different food choice may explain the synchronism that does not necessarily mean a common life. Comparison of techniques of food processing shows variations between chimpanzee populations. Some ignore the nuts, others only eat the outer energy-rich husk and others use stone tools to extract the protein-rich kernel (McGrew, 1986).

We can imagine *H. habilis* settling in a territory already inhabited by *A. boisei*. Rather than exterminating *A. boisei*, *Homo* would have used him as a vanguard. This arrangement may be a good example of opportunism by our ancestors and explain the extinction of *A. boisei* and the success of *Homo* as a consequence of the variability of early hominid behavior in a same environment.

Source : MNHN, Paris

FIG. 15. — Etched enamel is observed in *Pongo* after unripe fruit action. Buccal side of the occlusal enamel of a lower right first molar × 50.

FIG. 16. — Buccal surface of the first right lower molar of Olduvai Hominid 7, occlusal margin at top. Magnification 50 gives evidence that all crown surfaces are eroded.

Source : MNHN, Paris

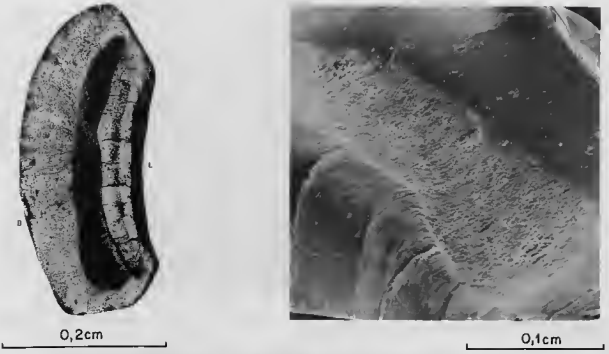

FIG. 17. — Photonic transmitted light and scanning observation of the characteristic wear pattern in front teeth of *Homo habilis* at Olduvai. Olduvai Hominid 7 central lower right incisor.
B = buccal; L = lingual.

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Source : MNHN, Paris

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Source : MNHN, Paris

Interstitial and Occlusal Wear of First Molar Teeth in San (Bushmen)

J. F. VAN REENEN & S. G. REINACH

ABSTRACT

Occlusal and interstitial wear of first molar teeth was studied in three groups of Bushmen, namely, a group in Botswana, one in Bushmanland and the other from Angola (Vassekela Bushmen). Interstitial contact between teeth moved up to the marginal ridge at an early age. More wear occurred in mandibular than maxillary teeth. Most of the first molars were in good alignment in the dental arcades but the Vassekela Bushmen, who had intermarried with Angolan blacks, had the highest frequency of first molars out of alignment. This was more frequent in males than females. Buccal rotation of molars tended to increase with age and particularly in the case of mandibular molars. Lingual inclination of mandibular molars dcereased with age. Chipping occurred more on right than left side, was more marked in mandibular teeth and the frequency also increased with age. Occlusal wear of first molars occurred more frequently in females than in males, more on the right side and more in mandibular teeth. The straight pattern of interstitial wear was the most frequent to be observed and especially on the mesial surfaces of first molars. The concave pattern of interstitial wear appeared to be related to primitiveness. During the initial stages of occlusal wear, facets developed and then pits on the enamel surface. Dentine was not exposed at this stage. It is suggested that there is a close association between the development of occlusal wear facets, occlusal pit formation, occlusal wear pattern and mesial and distal interstitial wear patterns. The optimum relationship between these variables seemed to exist when the

RÉSUMÉ

Les auteurs ont étudié l'usure occlusale et interstitielle des premières molaires dans trois groupes de Boschimans, au Bostwana, au Bushmanland et en Angola (Bushmen Vassekela). Le contact interstitiel entre les dents se déplace vers le bord marginal á un âge précocc. L'usure est plus marquée sur les dents mandibulaires que sur les dents maxillaires. La plupart des premières molaires sont bien alignées sur l'arcade dentaire sauf chez les Boschimans Vassekela, métissés avce les Noirs de l'Angola, chez qui on a trouvé la plus forte frèquence de molaires non alignées; ce fait est en outre plus frèquent chez les hommes que chez les femmes. La rotation buccale des molaires tend á croître avec l'âge ; ceci est particulièrement vrai des molaires inférieures. L'inclinaison linguale de ces molaires inférieures diminue avec l'âge. Les dents ayant perdu des éclats sont plus nombreuses à droite qu'á gauche, plus en bas qu'en haut, et plus nombreuses aussi avec l'âge. L'usure occlusale des premières molaires est plus fréquente chez les femmes que chez les hommes, plus á droite qu'á gauche et plus fréquente sur les dents inférieures. L'usure interstitielle la plus couramment observée est le mode rectiligne, et ceci plus spécialement sur les surfaces mésiales des premières molaires. Le mode concave d'usure interstitielle semble lié á un état primitif. Durant les premiers stades d'usure occlusale apparaissent des facettes, puis des fossettes sur la surface de l'émail. A ce stade la dentine n'est pas exposée. Les auteurs suggèrent l'existence d'un lien étroit entre le développement de facettes d'usure occlusale, la formation de fossettes

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Paris, ISBN 2-85653-148-2

Source : MNHN, Paris

following were present: 6 wear facets, 4 pits, third stage of occlusal wear, the convex pattern distally and straight pattern of interstitial wear mesially. Facet formation is thought to be due to attrition, and pit formation to be caused by abrasion. Exposure of dentine and fossa formation by coalescence of pits reduce articulation between maxillary and mandibular teeth. Differences in chewing patterns may account for variations in wear patterns. It is suggested that a predominance of either side to side, antero-posterior or intrusive tooth movements accounts for differences in interstitial wear patterns. The coarseness of the diet, masticatory preference areas and the individual chewing patterns are likely to be the three major factors which produce differences in occlusal and interstitial wear patterns.

occlusales, le mode d'usure occlusale et le mode d'usure interstitielle mésiale et distale. Le rapport optimal entre ces variables semble exister dans le cas suivant : 6 facettes d'usure, 4 fossettes, troisième stade d'usure occlusale, mode convexe distalement et rectiligne mésialement d'usure interstitielle. La formation de facettes est considérée comme étant due à l'attrition, et la formation de fossettes à l'abrasion. L'affleurement de la dentine et la formation de fosses par coalescence des fossettes réduisent l'articulation entre les dents maxillaires et mandibulaires. Des différences dans le mode masticatoire peuvent être responsables des variations du mode d'usure. Les auteurs suggèrent que la prédominance des mouvements latéraux, antéro-postérieurs ou intrusifs des dents, rend compte des différents modes d'usure interstitielle. Le caractère abrasif de la nourriture, les aires masticatoires préférentielles et le mode de mastication individuel sont vraisemblablement les trois principaux facteurs qui provoquent des différences dans les modes d'usure occlusale et interstitielle.

Introduction

Teeth are the masticatory tools of man and animals. They are put to use soon after their eruption into the mouth and continue to be useful until they are lost. In man the crowns of teeth are covered with enamel, a hard durable substance which is extremely efficient in meeting the functional demands made upon the dentition.

Like all tissues of the body, enamel wears. Unlike other tissues, however, it cannot be replaced or repaired by normal body mechanisms and its loss by wear or other means is permanent.

Wear occurs soon after tooth eruption and this changes the shape of the tooth surface (Van Reenen, 1982). The pattern of wear produced is an indication of the functional demands made upon the teeth. Unfortunately the aetiological factors responsible for tooth wear are not well understood. There are at least 4 known processes which contribute to the loss of tooth substance. These may act singly or in combination with each other.

Firstly, attrition or the wearing away of one tooth surface while rubbing against another (Scott & Symons, 1964). In the case of occlusal attrition, this produces wear facets on the two opposing teeth, the one on the maxillary tooth corresponding with the one on the opposing mandibular tooth. When interproximal attrition occurs, the mesial and distal surfaces of adjoining teeth wear at the point or area of contact producing facets of wear on both teeth.

Secondly, abrasion or the loss of tooth substance caused by external physical agencies such as gritty materials in food (Moorrees, 1957; Scott & Symons, 1964). The teeth are out of occlusion when this type of wear occurs because the abrading material prevents intimate contact. Similarly, in the case of interproximal abrasion, the mesial and distal surfaces of two opposing teeth must become separated temporarily in order to allow the abrasive materials to interpose between the teeth.

Thirdly, erosion or the loss of tooth substance by chemicals, usually acids other than those produced by bacteria. The lesions tend to be smooth, rounded and polished in appearance (Smith, 1975; Eccles, 1982). They can occur on any tooth surface presumably also interstitially, although this would be considered unusual.

Fourthly, pressure chipping, flaking, fracturing or splintering of crown surfaces as a result of marked crushing forces applied to the teeth (Pedersen, 1949; Turner & Codien, 1969). These are traumatic lesions which have been reported to occur in Aleuts, Eskimos and Indians (Turner & Codien, 1969).

Some of the effects of wear on the teeth of

Source : MNHN, Paris

Bushmen have been described by Van Reenen (1964, 1982). These people, like the Eskimos, show tooth wear at an early age. It is often marked by the time they reach adulthood and the crowns of the teeth may be completely worn away by the time they reach old age. Van Reenen (1982) showed that crown height diminished the most and the labiolingual lengths the least as a result of wear. As far as individual teeth are concerned, the maxillary first incisors tend to show more wear than any of the other maxillary teeth. Crown height of the mandibular first incisors also shows most wear but the mesiodistal and labiolingual dimensions of first mandibular molars reduce more with age than the other mandibular teeth. Wear tends to be more marked in males than in females. The mesiodistal dimensions reduce by approximately 20 per cent and crown height by almost 50 per cent by the time secondary dentine is exposed.

The patterns of occlusal and interproximal wear were not studied by Van Reenen (1964, 1966, 1982). The present study was undertaken to describe these wear patterns in San and to speculate on the genesis of them. The investigation was limited to a study of first molars because they show more wear than any of the other posterior teeth.

Material and Method

Plaster casts of the dentitions were used in this study. The material was obtained during expeditions to the Central Kalahari Desert of Botswana in 1959 and 1964 and also during a recent expedition (1985) to Bushmanland, a part of the desert extending into the north eastern corner of South West Africa. The material collected in 1959 and 1964 formed Group 1 of the present study (141 casts). This group is referred to as 'Kung '64 in the text although it comprised other clans as well. A group of 'Kung Bushmen examined in Bushmanland in 1985 were placed in Group 2 (67 casts) and Vassekela Bushmen who were of Angolan origin also examined in 1985 were allocated to Group 3 (77 casts).

Impressions were taken in alginate of the dentitions of all subjects studied. Casts were prepared immediately in artificial stone. Groups 1 and 2 comprised males and females but Group 3, young male subjects only. The ages of the Bushmen examined had to be estimated. The subjects used in this study fell into 4 age groups namely adolescents, or young people with permanent teeth but without third molars, young adults in whom the third molars had erupted, middle aged people estimated to be over 40 years of age and old aged people estimated to be over 60 years of age.

The following methods of scoring were adopted:

Height of contact with adjacent tooth (Fig. 1)

1. No contact as a result of space or unerupted tooth = O
2. Contact near gingival margin = GM
3. Contact at marginal ridge level. Adjacent marginal ridges of equal height = MR
4. Contact below marginal ridges of adjacent tooth *
5. Contact above marginal ridges of adjacent tooth *
6. Functional space has developed as a result of interproximal wear. This space presumably closed when the tooth occludes during chewing *
7. Contact lost due to severe occlusal wear = L

(* Frequencies were small and these values were discarded in tables of result).

Position of contact with adjacent tooth (Fig. 2)

B. Tooth bucally placed in arcade
C. Central — masticatory grooves coincide
L/P. Tooth lingually or palatally placed in arcade

Chipping of margin (Fig. 3)

O. No chipping
+. Slight chipping
++. Marked chipping

Occlusal wear pattern of maxillary first molar tooth (Fig. 4)

1. Wear facets on cusps, no dentine exposed.
2. Wear facets have almost obliterated cusps, pits may have developed near crests of cusps.
3. Cusps almost eliminated and transverse ridge flattened by wear but fissures still present; pits now well developed in vicinity of cusps and dentine usually exposed.

Source : MNHN, Paris

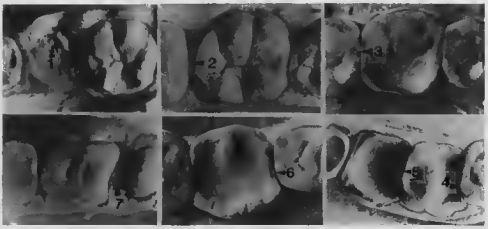

FIG. 1. — Height of contact with adjacent tooth.
1 = no contact as a result of space or unerupted tooth; 2 = contact near gingival margin; 3 = contact at marginal ridge level. Adjacent marginal ridges of equal height; 4 = contact below marginal ridge of adjacent tooth; 5 = contact above marginal ridge of adjacent tooth; 6 = functional space has developed; 7 = contact lost due to severe occlusal wear.

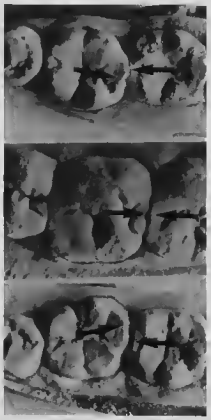

FIG. 2. — Position of contact with adjacent tooth.
B = tooth buccally placed in arcade; C = central — masticatory grooves coincide; L/P = tooth lingually or palatally placed in arcade.

Source : MNHN, Paris

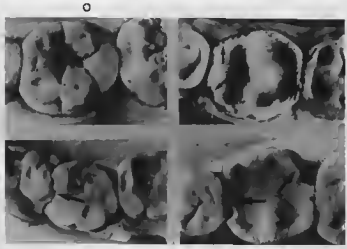

FIG. 3. — Chipping of margin.
O = no chipping; + = slight chipping; + + = marked chipping.

4. Pits enlarged and usually confluent in region of mesiopalatal cusp; dentine well exposed but evidence of enamel fissures still present.
5. Confluence of mesiopalatal and mesiobuccal pits well established producing a shallow valley of exposed dentine; evidence of fissures still present on enamel remnant which is high to valley of exposed dentine.
6. Valley of exposed dentine now well developed but some enamel present in region of distobuccal cusp; evidence of fissures usually present on enamel surface.
7. Deep valley of exposed dentine now extends over more than half of occlusal surface; remains of distobuccal cusp and enamel fissures now only slight.
8. Occlusal surface now one single valley of exposed dentine with no evidence of distobuccal cusp or enamel fissures. Secondary dentine usually exposed.

OCCLUSAL WEAR PATTERN OF MANDIBULAR FIRST MOLAR TOOTH (Fig. 5)

1. Slight evidence of wear by facet formation.
2. Wear facets have developed on cusps and pitting of enamel may be present near cusp crests.
3. Pits enlarged and dentine usually exposed by pits; cusps flattened but central fissure still present.
4. Cusps almost eliminated, pits of exposed dentine well developed; central fissures still present.
5. Pits well developed and fissures almost eliminated by wear.
6. Either mesial and/or distal 2 pits now confluent; remains of fissures may be present.
7. Further confluence of pits but ridge or island of enamel remains centrally; evidence of fissures may be present.
8. Whole occlusal surface now one single valley of exposed dentine; small enamel island may be present; secondary dentine usually exposed.
9. Pulp chamber exposed.
10. Wear down to root level and root canals exposed.

INTERSTITIAL WEAR PATTERN (Fig. 6)

1. Convex contact area
2. Straight contact area
3. Slight concave contact area
4. Definite concave contact area *
5. Markedly concave contact area *
6. S-shaped or irregular contact area

(* These categories were usually associated with a functional space).

Source : MNHN, Paris

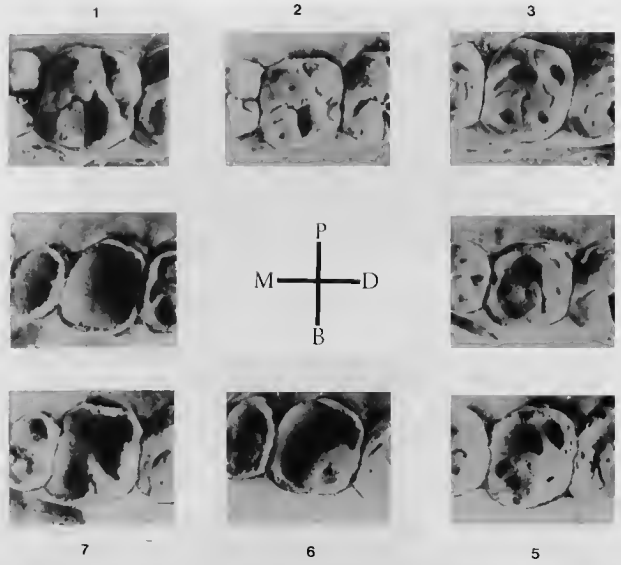

FIG. 4. — Occlusal wear pattern of maxillary first molar tooth.

1 = wear facets on cusps, no dentine exposed; 2 = wear facets have almost obliterated cusps, pits may have developed near crests of cusps; 3 = cusps almost eliminated and transverse ridge flattened by wear but fissures still present; pits now well developed in vicinity of cusps and dentine exposed; 4 = pits enlarged and usually confluent in region of mesiopalatal cusp; dentine well exposed but evidence of enamel fissures still present; 5 = confluence of mesiopalatal and mesiobuccal pits well established producing a shallow valley of exposed dentine; evidence of fissures still present on enamel remnant which is high to valley of exposed dentine; 6 = valley of exposed dentine now well developed but some enamel present in region of distobuccal cusp; evidence of fissures usually present on enamel surface; 7 = deep valley of exposed dentine now extends over more than half of occlusal surface; remains of distobuccal cusp and enamel fissures now only slight; 8 = occlusal surface now one single valley of exposed dentine with no evidence of distobuccal cusp or enamel fissures. Secondary dentine usually exposed.

Source : MNHN, Paris

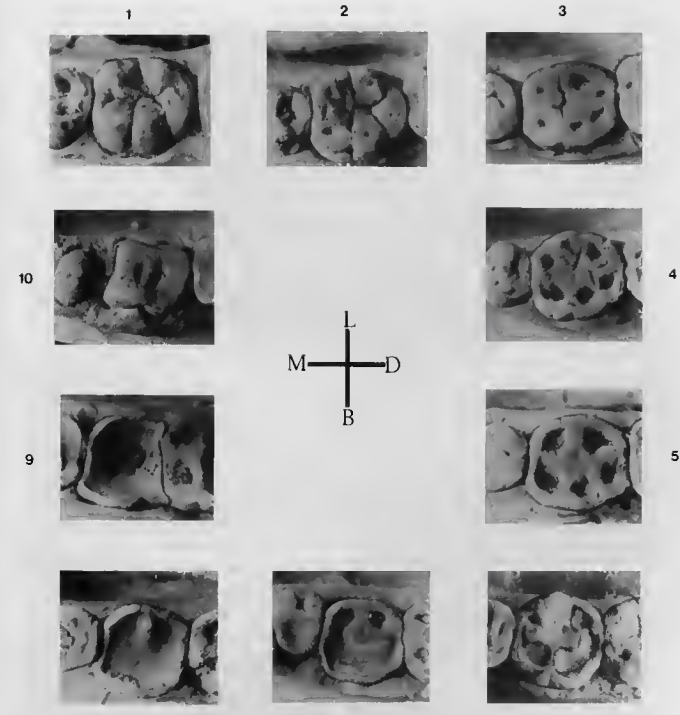

FIG. 5. — Occlusal wear pattern of mandibular first molar tooth.

1 = slight evidence of wear by facet formation; 2 = wear facets have developed on cusps and pitting of enamel may be present near cusp crests; 3 = pits enlarged and dentine exposed; cusps flattened but central fissure still present; 4 = cusps almost eliminated, pits of exposed dentine well developed; central fissures still present; 5 = pits well developed and fissures almost eliminated by wear; 6 = either mesial and/or distal 2 pits now confluent; remains of fissures may be present; 7 = further confluence of pits but ridge or island of enamel remains centrally; evidence of fissures may be present; 8 = whole occlusal surface now one single valley of exposed dentine; small enamel island may be present; secondary dentine usually exposed; 9 = pulp chamber exposed; 10 = wear down to root level and root canals exposed.

Source : MNHN, Paris

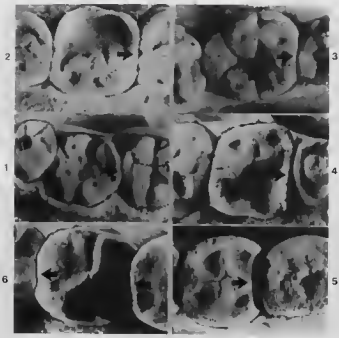

FIG. 6. — Interstitial wear pattern.
1 = convex contact area; 2 = straight contact area; 3 = slight concave area; 4 = definite concave area; 5 = markedly concave contact area; 6 = S-shaped or irregular contact area.

ANALYSIS OF DATA

This was undertaken in two parts. Firstly analysis of the data collected for the total sample was undertaken. Secondly 52 young adult male subjects belonging to the Vassekela group who showed minimal to moderate signs of tooth wear, were selected and data collected from them were analysed separately in order to gain a better understanding of the initial wear changes in the dentition. In this group, the number of wear facets on each first molar and number of pits which had developed on the occlusal surface were counted and compared with other variables.

STATISTICAL ANALYSIS

The data was set out in two-way tables with the groups in one direction and all the other variables in the other direction. The Chi-squared test was used to determine whether a statistically significant relationship between the two variables in the table existed (Afifi & Azen, 1979).

RESULTS

A. *Total sample*

SEX AND AGE DISTRIBUTION

The frequencies of these two variables are shown in Table 1.

HEIGHT OF CONTACT (Tables 2, 3 and 4).

The highest frequency of interstitial contact occurred at the marginal ridge (category 3) in all 3 groups (range 88.6-100.0 per cent). Loss of contact due to severe wear occurred more frequently in the !Kung '64 Bushman group than in the other groups, more frequently mesially than distally and more frequently in the mandibular than the maxillary teeth. This group had less contact with western civilisation.

Comparison of male and female values indicated a similar trend and shows that contacts were lost as a result of wear more frequently in females than in males.

Source : MNHN, Paris

Analysis of this variable by age tended to support the above observations but in addition showed that more wear occurred in the mandibular than the maxillary molars.

Position of contact (Tables 5, 6 and 7)

This was mostly central (range 60.3-96.4 per cent) (category 2) in all 3 groups indicating that the first molars were in alignment in the dental arcade of most subjects and especially in the 'Kung '64 group. There was a distinct tendency for irregularity of the first molar to occur more frequently in the 'Kung '85 and Vassekela '85 groups and particularly in the latter group. There was also a tendency for the right maxillary and left mandibular molars to show this irregularity and for a lingual or palatal inclination to occur except in the Vassekela '85 group where the left maxillary and right mandibular molars tended to show a higher frequency of buccal rotations than the other two groups.

An analysis of the data by sex supported these observations but indicated that twisting of molars occurred more frequently in males than females.

There was a distinct tendency for buccal inclination of molars to increase with age and particularly in the case of mandibular teeth. On the other hand the frequency of lingual twisting of mandibular molars tended to decrease with age. Analysis of the data by age again indicated that the maxillary right and mandibular left molars showed a greater tendency to rotation, either buccally or lingually, than the other two molars.

Chipping of margin (Tables 8, 9 and 10)

The frequency of mild chipping ranged from 4.7-21.5 per cent; was more marked in the 'Kung '64 Bushmen and least noticeable in the Vassekela '85 Bushmen; tended to occur more on the right than the left side and tended to be more marked in mandibular than maxillary teeth.

Analysis of chipping by age showed that the frequency increased progressively from adolescence to old age; confirmed that it was more marked on the right than the left side and also indicated that it was more marked in mandibular than maxillary molars.

Occlusal wear patterns (Tables 11, 12 and 13)

The sum of the 4 highest frequency values indicated that occlusal wear was highest amongst the 'Kung '64 group, intermediate in the 'Kung 85 group and least in the Vassekela '85 Bushmen. It also tended to be more marked on the right than the left sides.

Using the same method of evaluation, an analysis by sex showed that severe wear tended to occur more frequently in females than in males; more frequently on the right than the left side and that it was more severe in mandibular than maxillary first molars. Similarly, an analysis by age showed that the 4 highest frequency categories increased with age and wear tended to be higher on the right than the left sides.

Interstitial wear patterns (Tables 14, 15 and 16)

The frequencies of the straight interstitial wear pattern tended to be the highest of the 4 major categories. There was also a tendency for this pattern to occur more frequently on mesial than distal surfaces. An unexcepted finding was that this pattern occurred most frequently amongst the 'Kung '85 Bushmen, was intermediate in the Vassekela '85 group and had a lower frequency in the most primitive of the 3, the 'Kung '64 group. The frequency was higher in maxillary than mandibular teeth except in the case of the 'Kung '85 group where the opposite was true.

The next highest frequencies occurred for the convex category of contact. It was highest in the Vassekela '85, intermediate in the 'Kung '64 and lowest in the 'Kung '85 group. It occurred more frequently in maxillary than mandibular molars with the exception of the 'Kung '85 group where the frequency was higher in mandibular teeth. It was found more frequently distally than mesially and the frequency tended to be slightly higher on the right side.

The third highest frequencies occurred for the first concave category (3) of contact. This type of contact appeared to be directly related to primitiveness. The highest frequency was found in the 'Kung '64 group and the lowest in the Vassekela '85 group, the 'Kung '85 group occupying an intermediate position. In all 3 groups it had a higher frequency in mandibular than maxillary molars and occurred more often mesially than distally in the first molars of both jaws. The more advanced forms of this category of wear (4 and 5) showed low frequencies.

The S-shape or irregular contact was the least frequent of the 4 major categories of interstitial

Source : MNHN, Paris

wear. It was found more frequently in the 'Kung '85 group and least often in the Vassekela '85 group with the 'Kung '64 group occupying an intermediate position. It occurred slightly more frequently in maxillary than mandibular teeth and more frequently mesially in the maxillary and distally in the mandibular first molars.

An analysis by sex confirmed that the straight pattern of contact was the one most frequently encountered, followed by the convex pattern. Both patterns occurred more frequently in maxillary than mandibular molars, more frequently in males than females and more frequently mesially than distally in both the maxillary and mandibular first molars. This analysis also confirmed that the third most frequent or concave form of contact (3) occurred more frequently in mandibular than maxillary molars, more frequently mesially than distally in the first molars of both jaws and in contrast to the previous two patterns more frequently in females than in males.

The analysis by sex confirms the observations made previously that the S-shaped contact pattern is the least frequently encountered. Like the concave pattern, it occurred more frequently in females than in males, more frequently in the maxillary than in mandibular first molars and more frequently mesially in the maxillary and distally in the mandibular first molar teeth.

Table 16 demonstrates that in the analysis by age the frequency of the convex pattern of interstitial wear tended to be highest in adolescents, especially distally and in the mandibular molars. In the other age groups this pattern of wear was the second most frequent type encountered. As indicated above, the straight pattern of contact predominated in young adults, middle and old aged groups. The concave patterns of wear (3, 4, 5) were the third in order of frequency and tended to increase with age, especially mesially in mandibular first molars. The sample of middle (71) and old aged (27) subjects was small and the values on the tables may not accurately reflect the frequencies of this pattern especially as first molar teeth were sometimes lost in the mature age groups.

B. *Selected sample of young adults*

An attempt was made to establish whether an association existed between the variables: facets, pits, occlusal wear pattern, mesial and distal wear patterns. For purposes of this analysis, maxillary and mandibular and right and left side values were combined.

The distribution of values obtained by the interaction of two variables such as, for example, wear facets and pits, was determined and the actual values plotted on a graph. In most cases one value was greater than the rest. This formed the height or centre of the distribution. Surrounding this peak was a series of lower values. Similar values were joined forming contour lines which surrounded the peak. These incremental lines were prepared by use of a computer and showed the distribution of values (Z axis) for the two variables (X and Y axes). These surface plots showed the areas of maximal and minimal interaction.

Occlusal wear facets and occlusal pits.

The relationship between these two variables is demonstrated in Fig. 7 in which frequency contour lines are shown. This figure shows that wear facets develop before pits and that the maximum interaction of these two variables occurred at 6 wear facets and 4 pits.

Occlusal wear facets and occlusal wear patterns.

Fig. 8 shows that at least 2 wear facets had to develop before a first molar tooth was placed in the first category of occlusal wear and a minimum of 3 facets were present on teeth falling into the second and third occlusal wear patterns. The optimal expression of the interaction between these two variables appeared to have occurred at the stage when 6 wear facets and the third stage of occlusal wear had been reached.

Occlusal wear facets and mesial interproximal wear patterns.

Fig. 9 shows that a minimum of 2 occlusal wear facets were present on the occlusal surfaces of teeth which had convex and concave patterns of interstitial wear; a minimum of 3 wear facets on the teeth placed in the straight and a minimum of 4 wear facets on the teeth placed in the S-shaped category. For the convex pattern of interstitial wear the maximum frequency occurred when 6 occlusal facets had developed. This was also the case for the straight and S-shaped

Source : MNHN, Paris

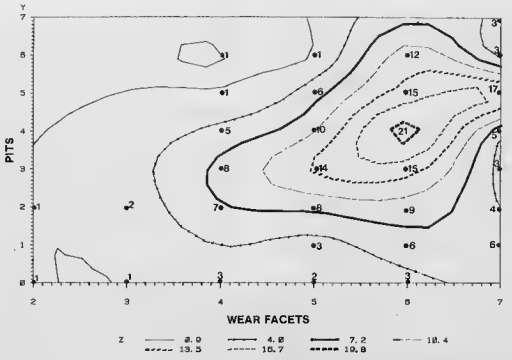

FIG. 7. — Surface plot showing frequencies of occlusal wear facets and pits. These two variables 'interact' maximally at 6 wear facets and 4 pits. Thus 21 first molars showed 6 wear facets and 4 pits; 15 first molars showed 6 wear facets and 5 pits; 15 first molars showed 6 wear facets and 3 pits etc.

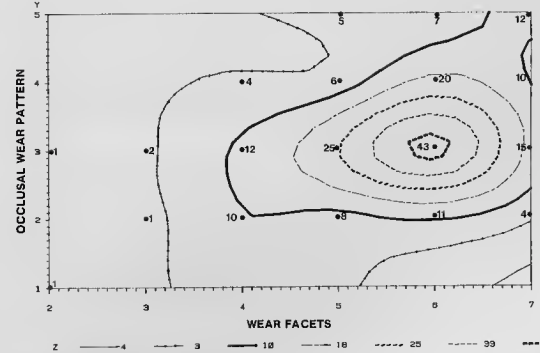

FIG. 8. — Surface plot showing frequencies of occlusal wear facets and actual wear patterns. These two variables interact maximally at 6 wear facets and the third category of occlusal wear pattern (cusps almost eliminated, fissures still present and dentine exposed). Thus 43 maxillary and mandibular molars showed 6 wear facets and were placed in the third category of occlusal wear pattern; 20 molars showed 6 wear facets and were placed in the fourth category of occlusal wear pattern (see figs. 4 and 5); 11 molars showed 6 wear facets and were placed in the second category of occlusal wear pattern etc.

Source : MNHN, Paris

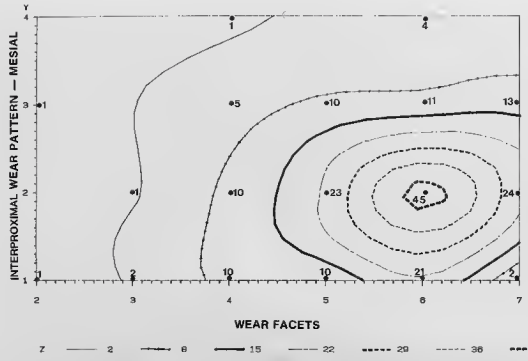

FIG. 9. — Surface plot showing frequencies of occlusal wear facets and mesial interproximal wear patterns (see legends of Figs. 7 and 8 for explanation).

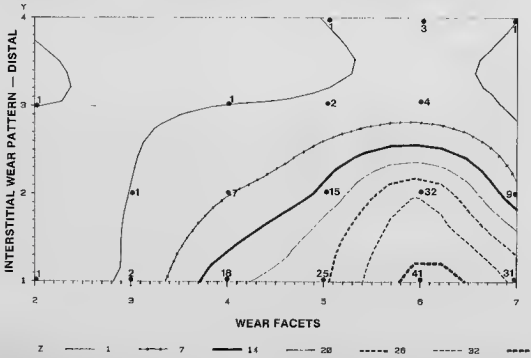

FIG. 10. — Surface plot showing frequencies of occlusal wear facets and distal interstitial wear patterns (see legends of Figs. 7 and 8 for explanation).

Source : MNHN, Paris

patterns. The concave pattern showed maximal expression at the 7 wear facet stage. The optimal expression of these two variables appeared when 6 occlusal wear facets had developed and the straight wear pattern was present.

Occlusal wear facets ano oistal interstitial wear patterns.

The peak interaction between these two sets of variables occurred with the convex wear pattern at the 6 occlusal facet stage. Fig. 10 shows that the optimal expression of all 4 wear patterns occurred when 6 wear facets have developed.

Occlusal pits ano occlusal wear patterns.

Fig. 11 shows that the first and second stages of occlusal wear developed before pits can be detected on the occlusal surfaces of first molars. The maximum expression of these two variables occurred when 3 pits had developed and the third stage of occlusal attrition had been reached.

Occlusal pits and mesial interstitial wear patterns.

Fig. 12 shows that the convex, straight and concave interproximal wear patterns are present in some first molar teeth before pits develop on their occlusal surfaces. The exception is the S-shaped pattern which was present in one case where 1 pit had developed occlusally. The maximum interaction of these 2 variables occurred for the straight pattern and 4 occlusal pits.

Occlusal pits and oistal interstitial wear patterns.

The interrelationship between these two variables appeared to be complex. Fig. 13 confirms that the wear patterns (except S-shaped one) were present before pits developed on the occlusal surfaces. These appeared to be two areas of maximum interaction, namely in the convex interstitial wear pattern when 3 and 5 pits had developed.

Occlusal wear and mesial interstitial wear patterns.

Fig. 14 shows that all 4 interstitial wear patterns found their maximum expression when the third stage of occlusal wear had occurred and the cusps of the first molar teeth had been eliminated. The optimal interaction appears to be in the case of the straight interproximal wear and the third occlusal wear patterns.

Occlusal wear and oistal interstitial wear patterns.

The optimal interaction of these two factors appeared to be at the convex interproximal and third occlusal wear pattern stages, or when the cusps had been removed by occlusal wear. Fig. 15 shows that the convex, straight and concave interproximal wear patterns occurred most frequently at the third stage of occlusal wear and that the S-shaped pattern occurred when the fourth stage of occlusal wear was reached.

Mesial ano oistal interstitial wear patterns.

Fig. 16 shows that the highest frequency recorded was a convex pattern distally and a straight pattern mesially. The optimum expression of all 4 patterns occurred on mesial surfaces when the convex pattern was present distally. The sequence of interstitial attrition patterns used in this study, namely, convex, straight, concave and S-shaped, appeared to be the ranking order for the distal surface of first molars.

Discussion

In a previous communication (Van Reenen, 1982) it was shown that wear of the teeth reduces their size. Implicit in this process is a change in tooth shape. The present study investigated some of the factors responsible for this change and attempts to trace the natural history of tooth wear.

Changes on the occlusal surfaces are easier to observe than those taking place interstitially. Modifications of tooth form however, proceed simultaneously on occlusal and interstitial surfaces, progress at different rates and form part of a multifactorial process.

Soon after eruption, teeth make contact occlusally with their counterparts in the opposite jaw and interstitially with adjacent teeth. In the case of first permanent molars the initial contact is minimal and limited to a few points occlusally and a point on the mesial surface. Wear begins soon after eruption (Van Reenen, 1982) and

Source : MNHN, Paris

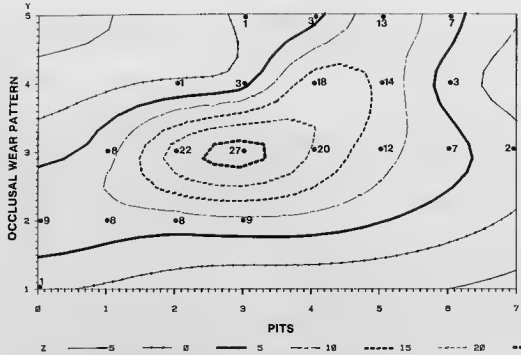

FIG. 11. — Surface plot showing frequencies of occlusal pits and occlusal wear patterns (see legends of Figs. 7 and 8 for explanation).

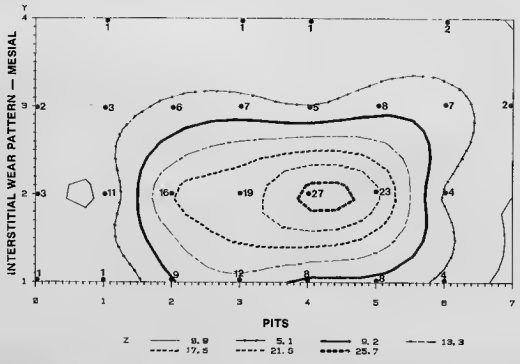

FIG. 12. — Surface plot showing frequencies of occlusal pits and mesial interstitial wear patterns (see legends of Figs. 7 and 8 for explanation).

Source : MNHN, Paris

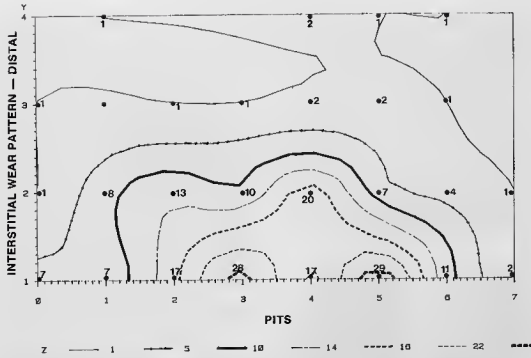

FIG. 13. — Surface plot showing frequencies of occlusal pits and interstitial distal wear patterns (see legends of Figs. 7 and 8 for explanation).

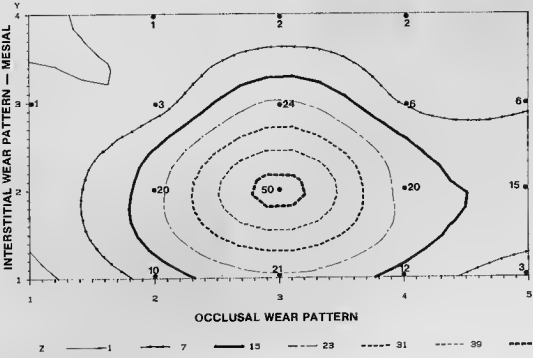

FIG. 14. — Surface plot showing frequencies of occlusal wear and mesial interstitial wear patterns (see legends of Figs. 7 and 8 for explanation).

Source : MNHN, Paris

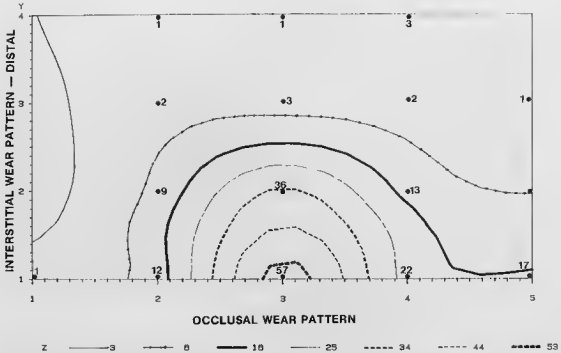

FIG. 15. — Surface plot showing frequencies of occlusal wear and interstitial distal wear patterns.

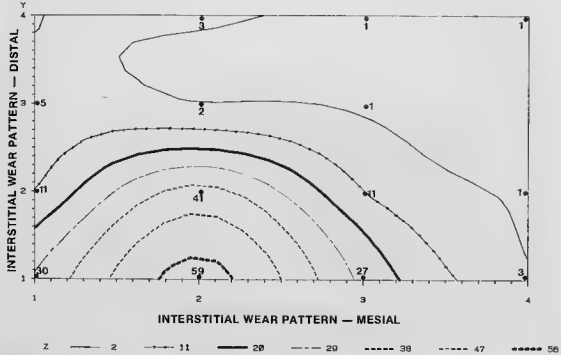

FIG. 16. — Surface plot showing frequencies of mesial and distal interstitial wear patterns (see legends of Figs. 7 and 8 for explanation).

Source : MNHN, Paris

points of contact develop into facets of contact. This improves tooth articulation both occlusally and interstitially.

Facets of wear develop on cusp inclines occlusally and between two adjacent teeth interstitially. They are flat and have a smooth, well polished, shiny appearance. Attrition is probably the major factor responsible for producing them although abrasion may help the process.

The establishment of occlusion is a new and extremely important experience for the child. Experiments are undoubtedly undertaken by the child to familiarise himself with the capabilities of this new masticatory tool. Initially contact may be better in one area of a tooth than another. Preference is likely to be given to such an area and to the right or the left side of the mouth, thereby establishing a chewing pattern and at the same time a wear pattern. In the case of Bushmen who consume hard, fibrous, gritty foods, abrasion will be most marked in masticatory preference areas.

Fig. 17 shows that wear facets preceded pit formations. The maximum interaction between these two variables takes place at 6 wear facets and 4 pits. All optimum pit frequencies occur at the 6 wear facet stage. For instance the frequencies for 3 and 5 pits were the same and were highest at the 6 wear facet stage. The frequencies for 2 and 6 pits were also highest at the 6 wear facet stage.

As the size of facets increases the size of cusps are reduced. Eventually all the cusps are eliminated and the occlusal surface is reduced to a single plane. This is covered by enamel but areas of dentine exposure break this plane (Fig. 17). In Bushmen this stage seems to terminate the active phase of occlusal attrition. Pit development followed facet formation (Fig. 18). Small microscopic defects or shallow fossae were visible on cusp inclines prior to overt pit formation. These defects were observed near the crests of cusps in the areas associated with the sites of pit formation. It is suggested that these shallow fossae develop into pits. Initially, pits are defects in enamel and dentine is not exposed. In this regard they differ from the defects described in Murphy (1959, 1968). There appears to be a close association between pits and facets because the number of pits eventually formed tended to coincide with the number of wear facets produced.

FIG. 17. — Cusps of first and second maxillary molars reduced to a single plane. Four pits exposing dentine present on first molar and one pit on second molar. Note interstitial contact between first and second molar is straight pattern but is irregular. It is suggested that this irregularity is due to abrasion.

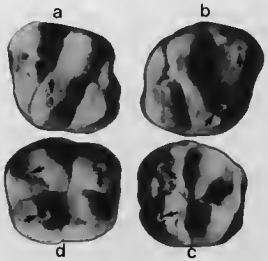

FIG. 18. — Early stages of pit formation; a and b are maxillary and c and d mandibular first molars. Pits indicated by arrows.

Pits are round concave fossae with smooth rounded edges. It is not clear how they originate but developmental defects in the enamel and trauma are two possibilities. It is suggested that once established their growth is caused by abrasion. These hollows are ideal areas for stagnation of abrasive and other particles consumed in the diet. During mastication these particles help to abrade the surface of the defect and thereby to increase the depth of the pits. A viscious circle of events is established which eventually terminates in the formation of one large fossa of dentine when this stage is reached. Articulation with the opposing tooth is reduced and some areas of the occlusal surface are separated by hollows from the opposing tooth surface. It would seem that

Source : MNHN, Paris

this particular wear process is not related to tooth contact, suggesting that abrasion rather than attrition is responsible for the wear (Fig. 19).

FIG. 19. — Maxillary premolar and molar teeth showing areas of exposed dentine which do not articulate with opposing mandibular teeth.

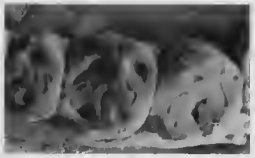

FIG. 20. — First maxillary molar shows straight interproximal pattern mesially and convex pattern distally. It is suggested that irregular shape of both surfaces is due to interproximal abrasion caused by sand or other particles lodging between teeth.

The scheme for the initial stages of the occlusal wear proposed in this study is based on facets of wear and pit formation. Fig. 8 shows that at the third stage, an average of 6 wear facets were present on the majority of molars (maxillary and mandibular) studied. This is the stage when cusps are flattened and almost eliminated. Fig. 11 shows that at this stage the majority of molars had developed 3 pits although a fair number of first molar teeth have either 2 or 4 pits and some 5-7 pits. Fig. 14 and 15 take the association further and show that at the third stage of occlusal wear the majority of first molars showed the second pattern of interstitial wear mesially (straight) and the first pattern distally (convex).

The straight interstitial wear pattern on the mesial surfaces of first molars was associated in the majority of subjects with 6 wear facets (Fig. 9), 4 pits (Fig. 12) and the third stage of occlusal wear (Fig. 14).

On distal surfaces the convex pattern of interstitial wear predominated and this was associated with 6 wear facets in the majority of cases (Fig. 10), either 3 or 5 pits (Fig. 13) and again the third stage of occlusal wear (Fig. 15).

Comparison of mesial and distal interstitial wear patterns (Fig. 16) shows that the second category (straight) occurred mesially and the first category (convex) distally in the majority of first molars (Fig. 20).

The information summarized in Figs. 7-16 therefore suggests that a close association exists between wear facets, occlusal pits, occlusal wear patterns, mesial and distal interstitial wear patterns.

With the loss of cusps and the exposure of dentine, the advanced stages of wear are reached. It is suggested that abrasion plays a major part in promoting the progress of wear in these stages. There is evidence that food and abrasive particles become lodged interstitially in the early stages of wear. Coarse abrasive materials such as sand or hard gritty particles derived from the woody shells of nuts lodge between the teeth, cause a localised area of abrasion and may be responsible for the irregular contact edges sometimes observed. A close inspection of interstitial surfaces shows that the margins were seldom entire, were frequently irregular in outline and were often dentate in appearance (Fig. 20) suggesting that it could be caused by abrasive particles lodged between the teeth.

Mild and marked forms of chipping were observed in a relatively small number of subjects (Fig. 21). Abrasion and other wear processes would tend to eliminate the evidence of chipping and it seems likely that this factor was more important in the general wear process than is indicated in Tables 8, 9 and 10.

FIG. 21. — First and second mandibular molars show advanced stage of wear. Second molar shows chipping of distal surface.

Source : MNHN, Paris

Bushmen use their teeth as tools and are able to crack the very hard shells of nuts between their molars. This practice is likely to cause chipping and may even be responsible for trauma to enamel which initiates the development of pits on the occlusal surfaces.

The initial stages of wear appeared to proceed quickly as shown by the observation made in Tables 2, 3 and 4. Interstitially attrition reduces the mesial and distal surfaces and thereby wears the contact points at the gingival margin into contact areas which extend to the marginal ridge. This process took place more rapidly in the primitive groups ('Kung '64), occurred more frequently mesially than distally and more frequently in the mandibular than the maxillary first molars. The mesial force vector pushes the mesial surface of the first molar forward against the second premolar and this results in more rapid wear of this surface (Wolpoff, 1971).

Interstitial contact areas were classified according to a scheme proposed by Patricia Smith after she had examined some of the casts ('Kung '64) used in this study. This scheme was later used by Kieser, Groeneveld & Preston (1985) in an investigation of a group of Lengua Indians. In their study the straight pattern of contact was the most frequent in the younger age groups and this form was rapidly worn into the concave or sinuous (S-shaped) forms. In the present study the convex pattern predominated in the adolescents and the straight pattern had the highest frequency in young adults, middle and old aged groups. It had a higher prevalence in maxillary first molars and a higher frequency mesially. In the Lengua Indians the opposite appears to exist. This suggest that the interproximal wear patterns of different race groups varies.

The transition from one interproximal wear pattern to another as appears to be the case in Lengua Indians (Kieser, Groeneveld & Preston, 1985) is not such an obvious feature of the Bushman dentition. It seems that in Bushmen the convex form changes to either a straight, or a concave or a S-shaped form. There is a tendency for the concave pattern to increase with age and with primitive dietary habits. This pattern occurred more frequently in mandibular than maxillary molars and was encountered more often mesially than distally (Fig. 22).

Unlike the Lengua Indians the S-shaped contact in Bushmen did not tend to increase with age.

FIG. 22. — Concave interproximal wear pattern mesially on mandibular first molar. Straight pattern distally is also developing into concave pattern. Note spacing mesially, suggesting first molar tips forward during function producing concave wear surface.

This type of contact was seldom encountered in adolescents and its frequency was low in the adult age groups.

The present study therefore suggests that the chewing patterns in Bushmen differ from those of the Lengua Indians. These chewing patterns would influence the movement of individual teeth which in turn would influence the interproximal wear pattern.

It seems likely that several types of tooth movement occur in Bushmen. Lateral or side to side movement as described by Wolpoff (1971) is probably the most frequent to occur. Wolpoff (1971) points out that a lateral component of force normally results from chewing. This component is produced by the lateral angulation of teeth and by jaw motions. He shows, however, that the magnitude of interstitial wear is directly related to the mesial force vector or to how hard the teeth push on each other. He describes in detail the factors responsible for this force.

This side to side movement will wear convex facets into straight contact areas, provided the two adjacent tooth surfaces move separately, first the one then the other in the same or in opposite directions. Teeth have more freedom to undertake this type of movement than any other type of movement because there is less resistance offered to it.

The wear produced would tend to be due to attrition although fine abrasive particles would assist the process. Separation of teeth by this wear would be prevented by the mesial migration of the distal tooth due to the mesial vector of force (Wolpoff, 1971).

Although it does not appear to have been

Source : MNHN, Paris

described, anteroposterior movement of first molars is likely to occur in some Bushmen subjects. This type of movement may occur less frequently than lateral movement. Close contact with adjacent teeth either mesially or distally would tend to prevent this movement unless the adjacent teeth also move forward or backward. It could also occur when intrusion of the tooth occurs on the side to which it moves. When this type of movement occurs the interproximal surface where it takes place will tend to wear concave. Evidence of the occurrence of this movement in Bushmen is the spacing between teeth which is sometimes associated with it and referred to as a functional space in this paper (Figs. 20 and 22 — mesial surfaces of first molars).

The concave surface indicates that intimate contact exists during chewing and suggests that the tooth tilts forwards or backwards to establish the contact. Abrasive particles in the existing space would assist wear. Another phenomenon is that the margin of some molars is either higher or lower than the adjacent tooth. The frequencies for these contact relationships is low but is evidence that tilting of molars occurs.

Reference has already been made to intrusive movements. When a force is directed vertically onto a tooth it moves in that direction but does not immediately return to its former position (Mühlemann, 1967). This is probably the force to which teeth are most frequently subjected although it has been shown that axial loads induce much smaller tooth movements than horizontal thrusts (Mühlemann, 1967). When abrasive materials collect between teeth and this type of movement occurs, irregular margins would be produced as is shown in Figs. 23 and 24.

It is difficult to explain the S-shaped pattern of wear. This may be associated with complex rotational movements of the teeth or more simply by an irregular position of the tooth in the dental arcade. Tables 5, 6 and 7 show that a small percentage of first molar teeth were positioned either buccally or lingually. These cases were sometimes associated with S-shaped interstitial wear patterns (Fig. 25). Wolpoff (1971) also refers to this type of contact and states that "differences in the form of proximal contact stem from the interplay of horizontal force components mesial and lateral, resulting from both different patterns of occlusion and different combinations of mesial and lateral root angulations...". It would seem that the explanation for the S-shaped contact is related to the alignment of the affected tooth in the arcade or intrusive movements of the tooth.

FIG. 23. — Irregular interstitial margin mesially and distally on first maxillary molar. This pattern of wear cannot be produced by side to side or anteroposterior tipping movements. It is suggested that this wear is produced by intrusive movements. Note S-shaped pattern of wear is developing mesially and distally.

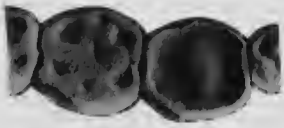

FIG. 24. — Irregular interstitial margin distally on second mandibular molar. It is suggested that this is produced by intrusive movements. Space has also developed permitting distal tipping of second and mesial tipping of third molar. Note S-shaped interstitial pattern of wear has developed distally on second molar.

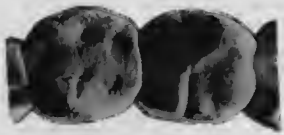

FIG. 25. — S-shaped interproximal wear patterns between mesial and distal surfaces of second mandibular molar. This pattern is associated with irregular alignment of the molar teeth.

Source : MNHN, Paris

The stages of occlusal attrition used in this study are similar to those described by Murphy (1959, 1968) in his study of Australian aboriginal skulls. His classification is based on exposure of dentine whereas the present one takes into account facet formation prior to dentine exposure at the one end and exposure of the pulp on the other end of the scheme.

Murphy (1959) points out that dentine becomes exposed at the centre of an attritional facet and that the exposed area becomes the central part of the facet. These exposed dentinal areas are sector-shaped in Australian aborigines. In Bushmen round pits are formed initially and they appear soon after facets have developed. At this stage they are in enamel and dentine is not exposed. The time interval between facet and pit formation appears to depend on the group examined. Sector-shaped areas sometimes develop in Bushmen (Fig. 20) but this is not a typical feature of exposed dentine areas.

The scheme put forward in Figs. 4 and 5 is based on the patterns which developed in the 'Kung '64 group. This group led a more primitive existence than other groups included in this survey and in them pit formation followed facet development far sooner than it did in the Vassekela '85 group who had more contact with the western way of life. The more detailed study of the initial stages of wear was undertaken on the latter group and it appears from Figs. 7 and 11 that the development of pits did not follow facet formation as soon as it did in the primitive 'Kung group as is shown in Figs. 4 and 5.

These observations suggest that the pattern of wear is influenced by diet and possibly genetic factors which determine the shape of a tooth. It is known that intermarriage with black tribes of Angola is responsible for some of the negro features present in Vassekela Bushmen. Negros usually have larger teeth than Bushmen.

The development of round pits in enamel appears to be the cardinal stage in the history of occlusal wear. It is suggested that these defects increase progressively by the action of abrasion until occlusal enamel is lost and a shallow fossa of exposed dentine remains. The stages between the development of the first pit and the final stage of both occlusal and interstitial wear seem to differ in detail in individuals and groups but not in direction of change.

Acknowledgements

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Source : MNHN, Paris

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Source : MNHN, Paris

TABLE 1. Sex and age distribution.

Variable	Category	Number	Percentage
Sex	Male	174	63
	Female	93	33,7
	Unknown	9	3,3
Age	Adolescent	19	6,8
	Young adult	158	56,2
	Middle aged	74	26,3
	Old aged	30	10,7

TABLE 2. Height of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
'Kung '64	O	0	0.7	0.7	0.0	0.7	0.0	0.8	1.5
	GM	3.6	2.9	3.6	2.9	3.6	1.5	3.0	0.8
	MR	94.2	94.9	93.5	96.3	90.6	94.9	88.6	92.4
	L	2.2	1.5	2.2	0.7	5.1	3.7	7.6	5.3
	N =	139	137	139	136	138	136	132	132
'Kung '85	O	0	0.0	1.4	8.2	2.9	1.4	1.5	3.0
	GM	1.4	0.0	0.0	0.0	0.0	0.0	0.0	1.5
	MR	98.6	100.0	98.6	91.8	95.7	97.1	97.0	93.9
	L	0	0.0	0.0	0.0	1.4	1.4	1.5	1.5
	N =	70	70	13	73	70	70	66	66
V '85	O	0	1.6	0.0	1.5	0.0	3.1	0.0	3.2
	GM	11.3	6.5	4.6	3.1	1.6	1.6	0.0	0.0
	MR	88.7	91.9	95.4	95.4	98.4	95.3	100.0	96.8
	L	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	N =	62	62	65	65	64	64	62	62
Probability*		0.019	0.050	0.486	0.004	0.201	0.264	0.022	0.240
Total N =		271	269	277	274	272	270	260	260

O = no contact
GM = gingival margin contact
MR = marginal ridge contact
L = contact lost
L = left side
R = right side
M = mesial
D = distal

'Kung '64 = 'Kung Bushman examined in 1964; 'Kung '85 = 'Kung Bushman examined in 1985; V '85 = Vassekela Bushman examined in 1985.

* Probability obtained from the Chi-squared test used in comparing groups.

Source : MNHN, Paris

TABLE 3. Height of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
Male	O	0	1.2	0.6	1.8	0.6	1.2	0.6	2.5
	GM	6.1	3.1	3.0	1.8	3.0	1.2	1.2	1.3
	MR	93.3	95.7	95.9	96.4	94.6	96.3	95.0	93.1
	L	0.6	0	0.6	0.0	1.8	1.2	3.1	3.1
	N =	164	163	169	167	166	164	161	160
Female	O	0	0	1.1	3.4	1.1	1.1	0	2.4
	GM	2.2	2.3	2.2	2.2	1.1	1.1	2.4	0.0
	MR	96.6	96.6	94.4	93.3	93.3	94.4	92.8	95.2
	L	1.1	1.1	2.2	1.1	4.4	3.3	4.8	2.4
	N =	89	88	90	89	90	90	83	84
Probability		0.168	0.411	0.504	0.704	0.395	0.716	0.761	0.799
Total N =		253	251	259	256	256	254	244	244

See legend, Table 2.

TABLE 4. Height of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
AD	O	0	0	0	0	0	0	0	5.9
	GM	15.8	12.5	15.8	12.5	26.3	11.8	16.7	5.9
	MR	84.2	87.5	84.2	87.5	73.7	88.2	83.3	88.2
	L	0	0	0	0	0	0	0	0
	N =	19	16	19	16	19	17	18	17
YA	O	0	0.7	0	0.7	0	1.3	0	2.0
	GM	5.3	2.6	2.0	1.3	0.6	0.6	0.7	0
	MR	94.7	96.7	97.4	98.0	99.4	98.1	99.3	98.0
	L	0	0	0.7	0	0	0	0	0
	N =	151	151	152	152	154	154	149	150
MA	O	0	1.4	0	2.7	2.9	0	1.5	3.0
	GM	2.9	2.8	2.7	2.7	0	0	0	1.5
	MR	95.7	95.8	95.9	94.5	94.3	98.6	90.9	89.4
	L	1.4	0	1.4	0	2.9	1.4	7.6	6.1
	N =	70	71	73	73	70	70	66	66
O	O	0	0	3.4	13.8	0	4.0	4.3	0
	GM	0	0	0	0	0	0	0	0
	MR	92.6	92.6	93.1	82.8	76.0	76.0	69.6	82.6
	L	7.4	7.4	3.4	3.4	24.0	20.0	26.1	17.4
	N =	27	27	29	29	25	25	23	23
Probability		0.005	0.004	0.006	0.000	0.000	0.000	0.000	0.000
Total N =		267	265	273	270	268	266	256	256

AD = Adolescent; YA = Young adult; MA = Middle aged; O = Old aged; and see legend, Table 2.

Source : MNHN, Paris

TABLE 5. Position of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
'K '64	B	3.6	1.5	5.1	2.9	4.4	12.6	3.0	4.5
	C	95.0	96.4	90.5	96.3	89.6	82.2	94.7	91.7
	L/P	1.4	2.2	4.4	0.7	5.9	5.2	2.3	3.8
	N =	139	137	137	136	135	135	133	132
'K '85	B	8.6	1.4	8.3	4.5	16.7	35.8	16.7	24.6
	C	85.7	85.7	79.2	85.1	74.2	62.7	78.8	72.3
	L/P	5.7	12.9	12.5	10.4	9.1	1.5	4.5	3.1
	N =	70	70	72	67	66	67	66	65
V '85	B	15.9	4.8	10.4	7.6	7.8	36.5	12.7	30.6
	C	82.5	87.3	77.6	83.3	73.4	60.3	76.2	62.9
	L/P	1.6	7.9	11.9	9.1	18.8	3.2	11.1	6.5
	N =	63	63	67	66	64	63	63	62
Probability		0.010	0.018	0.082	0.007	0.001	0.000	0.000	0.000
Total N =		272	270	276	269	265	265	262	259

B = buccal; C = central; L/P = lingual or palatal; and see legend, Table 2.

TABLE 6. Position of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
Male	B	9.8	2.5	8.9	4.8	11.0	30.2	11.6	21.3
	C	87.2	91.4	83.3	89.7	75.5	64.8	81.1	73.1
	L/P	3.0	6.1	7.7	5.5	13.5	4.9	7.3	5.6
	N =	164	163	168	165	163	162	164	160
Female	B	4.4	2.2	4.4	4.6	3.4	13.8	3.6	3.6
	C	93.3	91.0	86.7	90.8	93.1	83.9	96.4	94.0
	L/P	2.2	6.7	8.9	4.6	3.4	2.3	0	2.4
	N =	90	89	90	87	87	87	83	83
Probability		0.290	0.977	0.412	0.953	0.002	0.006	0.003	0.000
Total N =		254	252	258	252	250	249	247	243

See legends, Tables 2 and 5.

Source : MNHN, Paris

TABLE 7. Position of contact frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
AD	B	0	5.9	0	5.9	0	6.3	5.6	0
	C	100.0	94.1	89.5	94.1	89.5	81.3	94.4	93.8
	L/P	0	0	10.5	0	10.5	12.5	0	6.3
	N =	19	17	19	17	19	16	18	16
YA	B	11.8	2.0	9.0	4.5	8.5	28.3	9.3	19.3
	C	86.3	90.8	85.8	90.9	81.0	67.1	83.4	74.7
	L/P	2.0	7.2	5.2	4.5	10.5	4.6	7.3	6.0
	N =	153	153	155	154	153	152	151	150
B	O	2.9	2.9	5.6	5.8	9.0	20.3	7.4	12.1
	C	92.8	91.3	90.3	89.9	82.1	78.3	91.2	86.4
	L/P	4.3	5.8	14.1	4.3	9.0	1.4	1.5	1.5
	N =	69	69	71	69	67	69	68	66
O	B	3.7	0	3.6	0	13.0	20.8	9.5	13.0
	C	92.6	92.6	85.7	84.0	82.6	79.2	90.5	87.0
	L/P	3.7	7.4	10.7	16.0	4.3	0	0	0
	N =	27	27	28	25	23	24	21	23
Probability		0.049	0.703	0.231	0.224	0.784	0.177	0.928	0.155
Total N =		268	266	273	265	262	261	258	255

See legends, Tables 2 and 5.

TABLE 8. Chipping frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
'K '64	O	80.7	76.8	71.5	65.9
	+	16.4	19.6	20.4	21.5
	++	2.9	3.6	8.0	12.6
	N =	140	138	137	135
'K '85	O	76.8	78.1	77.9	67.2
	+	20.3	16.4	11.8	20.9
	++	2.9	5.5	10.3	11.9
	N =	69	73	68	67
V '85	O	90.5	89.4	93.8	93.5
	+	6.3	10.6	4.7	4.8
	++	3.2	0.0	1.6	1.6
	N =	63	66	64	62
Probability		0.246	0.170	0.005	0.001
Total N =		272	277	269	264

See legend, Table 2.

TABLE 9. Chipping frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
Male	O	81.2	81.5	78.7	73.8
	+	15.2	16.1	14.0	17.7
	++	3.6	2.4	7.3	8.5
	N =	165	168	164	164
Female	O	83.1	74.7	78.7	72.6
	+	14.6	19.8	14.6	14.3
	++	2.2	5.5	6.7	13.1
	N =	89	91	89	84
Probability		0.822	0.292	0.979	0.462
Total N =		254	259	253	248

See legend, Table 2.

Source : MNHN, Paris

TABLE 10. Chipping frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
AD	O	89.5	89.5	94.7	89.5
	+	10.5	10.5	5.3	0
	+ +	0	0	0	10.5
	N =	19	19	19	19
YA	O	86.8	84.4	86.2	80.1
	+	11.2	13.6	9.9	15.2
	+ +	2.0	1.9	3.9	4.6
	N =	152	154	152	151
MA	O	74.3	72.2	59.4	52.9
	+	21.4	22.2	27.5	27.9
	+ +	4.3	5.6	13.0	19.1
	N =	70	72	69	68
O	O	70.4	69.0	68.0	63.6
	+	22.2	24.1	16.0	18.2
	+ +	7.4	6.9	16.0	18.2
	N =	27	29	25	22
Probability		0.037	0.049	0.000	0.000
Total N =		268	274	265	260

See legends, Tables 2 and 5.

TABLE 11. Occlusal wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
K '64	1	8.6	8.0	5.8	6.6
	2	18.7	20.3	9.5	8.0
	3	18.0	16.7	16.8	16.8
	4	23.7	21.0	15.3	14.6
	5	18.0	19.6	11.1	20.4
	6	2.2	4.3	13.9	8.8
	7	4.3	4.3	9.5	13.1
	8	6.5	5.8	8.0	6.6
	9			2.2	3.6
	10			2.9	1.5
	N =	139	138	137	137
'K '85	1	8.6	9.6	8.7	6.0
	2	22.9	20.5	8.7	10.4
	3	15.7	16.4	15.9	14.9
	4	15.7	20.5	18.8	23.9
	5	24.3	21.9	20.3	17.9
	6	7.1	6.8	10.1	10.4
	7	2.9	2.7	5.8	7.5
	8	2.9	1.4	10.1	7.5
	9			1.4	1.5
	10			0.0	0.0
	N =	70	73	69	67
V '85	1	25.0	23.9	9.4	11.1
	2	36.3	36.7	43.8	42.9
	3	14.1	14.9	17.2	17.5
	4	4.7	4.5	23.4	19.0
	5	0.0	0.0	4.7	9.5
	6	0.0	0.0	1.6	0.0
	7	0.0	0.0	0.0	0.0
	8	0.0	0.0	0.0	0.0
	9			0.0	0.0
	10			0.0	0.0
	N =	64	67	64	63
Probability		0.000	0.000	0.000	0.000
Total N =		273	278	270	267

See legend, Table 2.

Source : MNHN, Paris

TABLE 12. Occlusal wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
Male	1	16.3	16.5	9.7	3.4
	2	35.5	34.7	21.8	12.4
	3	16.3	17.1	19.4	13.5
	4	13.9	14.1	18.8	19.1
	5	10.8	10.6	12.7	16.9
	6	3.0	3.5	8.5	11.2
	7	1.8	1.8	3.6	11.2
	8	2.4	1.8	4.2	7.9
	9			1.2	1.1
	10			0.0	3.4
	N =	166	170	165	165
Female	1	6.7	5.6	9.1	4.7
	2	18.0	20.0	21.2	11.6
	3	20.2	17.8	18.8	14.0
	4	22.5	23.3	18.2	19.3
	5	21.3	21.1	16.4	18.6
	6	2.2	4.4	6.1	7.0
	7	4.5	3.3	3.6	18.6
	8	4.5	4.4	4.8	2.3
	9			1.8	2.3
	10			0.0	1.2
	N =	89	90	89	86
Probability		0.005	0.006	0.015	0.006
Total N =		255	260	254	251

See legend, Table 2.

TABLE 13. Occlusal wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla		Mandible	
		L	R	L	R
AD	1	36.8	36.8	31.6	31.6
	2	36.8	36.8	15.8	21.1
	3	15.8	21.1	26.3	21.1
	4	5.3	0	15.8	10.5
	5	5.3	5.3	5.3	10.5
	6	0	0	5.3	5.3
	7	0	0	0	0
	8	0	0	0	0
	9			0	0
	10			0	0
	N =	19	19	19	19
YA	1	16.4	16.3	8.4	8.6
	2	40.8	41.2	26.0	24.3
	3	19.7	19.6	20.1	21.7
	4	17.1	16.3	24.7	23.0
	5	5.9	6.5	14.9	17.8
	6	0	0	5.2	3.3
	7	0	0	0.6	1.3
	8	0	0	0	0
	9			0	0
	10			0	0
	N =	152	153	154	152
MA	1	2.8	2.7	1.5	1.4
	2	9.9	12.3	5.9	5.8
	3	12.7	12.3	10.3	7.2
	4	23.9	23.3	8.8	11.6
	5	28.2	30.1	13.2	18.8
	6	8.5	8.2	23.5	14.5
	7	5.6	5.5	16.2	23.2
	8	8.5	5.5	17.6	13.0
	9			2.9	4.3
	10			0.0	0
	N =	71	73	68	69
O	1	0	0	0	0
	2	0	0	0	0
	3	7.4	3.4	0	0
	4	11.1	13.8	4.0	8.7
	5	40.7	34.5	20.0	13.0
	6	7.4	17.2	8.0	13.0
	7	14.8	13.8	20.0	21.7
	8	18.5	17.2	24.0	21.7
	9			8.0	13.0
	10			16.0	3.7
	N =	27	29	25	23
Probability		0.000	0.000	0.000	0.000
Total N =		269	274	266	263

See legends, Tables 2 and 4.

Source : MNHN, Paris

TABLE 14. Interstitial wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
'K '64	1	14.3	40.7	20.7	47.5	17.2	43.7	11.2	33.8
	2	52.1	43.1	38.6	35.3	33.6	28.9	42.5	36.8
	3	25.7	8.8	27.1	11.5	37.3	14.8	32.1	7.5
	4	2.1	0.0	4.3	0.0	9.0	3.7	6.0	3.8
	5	0.0	0.7	0.0	0.0	0.0	3.0	0.7	3.8
	6	5.7	7.3	4.3	5.8	2.2	5.9	7.5	14.3
	N =	140	137	140	139	134	135	134	133
'K '85	1	11.4	28.6	12.3	16.4	7.2	46.4	9.0	43.3
	2	65.7	64.3	53.4	76.7	50.7	37.7	46.3	52.2
	3	8.6	1.4	19.2	2.7	30.4	10.1	26.9	4.5
	4	2.9	0.0	1.4	0.0	2.9	0.0	7.5	0.0
	5	0.0	0.0	0.0	0.0	1.4	1.4	0.0	0.0
	6	11.4	5.7	13.7	4.1	7.2	4.3	10.4	0.0
	N =	70	70	73	73	69	69	67	67
V '85	1	35.9	37.5	40.9	45.5	12.9	69.4	3.4	71.2
	2	59.4	53.1	40.9	42.5	53.2	25.8	62.7	25.4
	3	1.6	6.3	12.1	10.6	29.0	1.6	25.4	0.0
	4	0.0	0.0	1.5	0.0	4.8	0.0	6.8	0.0
	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	6	3.1	3.1	4.5	1.5	0.0	3.2	1.7	3.4
	N =	64	64	66	66	62	62	59	59
Probability		0.000	0.145	0.001	0.000	0.011	0.013	0.214	0.000
Total N =		274	271	279	278	265	266	260	259

See legend, Table 2.

TABLE 15. Interstitial wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
Male	1	21.7	37.2	26.5	39.6	14.4	57.5	7.5	50.6
	2	59.6	51.2	43.5	47.3	49.4	30.6	55.0	38.0
	3	11.4	6.7	19.4	11.2	26.3	5.0	26.3	3.2
	4	1.2	0	3.5	0	5.6	1.3	5.0	0.6
	5	0	0.6	0	0	0.6	1.3	0.6	1.3
	6	6.0	4.3	7.1	1.8	3.8	4.4	5.6	6.3
	N =	166	164	170	169	160	160	160	158
Female	1	14.4	34.8	14.8	44.0	11.2	34.4	8.3	36.5
	2	54.4	48.3	44.0	41.8	33.7	33.3	39.3	36.5
	3	23.3	6.7	22.0	5.5	42.7	21.1	34.5	7.1
	4	3.3	0	2.2	0	9.0	3.3	8.3	3.5
	5	0	0	0	0	1.1	3.3	0	3.5
	6	4.4	10.1	12.1	8.8	2.2	4.4	9.5	12.9
	N =	90	89	91	91	89	90	84	85
Probability		0.067	0.468	0.503	0.021	0.049	0.000	0.206	0.045
Total N =		256	253	261	260	249	250	244	243

See legend, Table 2.

Source : MNHN, Paris

TABLE 16. Interstitial wear pattern frequencies expressed as percentages and total number in each group (N).

Group	Category	Maxilla				Mandible			
		LM	LD	RM	RD	LM	LD	RM	RD
AD	1	42.1	61.1	47.4	66.7	27.8	76.5	33.3	76.5
	2	47.4	38.9	31.6	27.8	44.4	11.8	55.6	17.6
	3	10.5	0	15.8	0	27.8	11.8	11.1	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	6	0	0	5.3	5.6	0	0	0	5.9
	N =	19	18	19	18	18	17	18	17
YA	1	22.9	42.1	24.7	46.1	15.8	61.8	5.4	56.1
	2	61.4	47.4	44.8	41.6	41.4	28.3	52.0	31.1
	3	9.8	5.9	21.4	8.4	34.9	3.3	28.4	4.7
	4	1.3	0	1.3	0	5.9	1.3	8.1	0.7
	5	0	0.7	0.0	0	0	0	0	0.7
	6	4.6	3.9	7.8	3.9	2.0	5.3	6.1	6.8
	N =	153	152	154	154	152	152	148	148
MA	1	7.0	27.1	17.8	24.7	7.6	30.9	8.8	17.9
	2	54.9	51.4	46.6	56.2	42.4	32.4	39.7	58.2
	3	21.1	11.4	17.8	13.7	34.8	25.0	35.3	7.5
	4	4.2	0	5.5	0	6.1	2.9	4.4	4.5
	5	0	0	0	0	1.5	2.9	1.5	1.5
	6	12.7	10.0	12.3	5.5	7.6	5.9	10.3	10.4
	N =	71	70	73	73	66	68	68	67
O	1	7.4	14.8	13.8	20.7	4.0	16.0	4.1	21.7
	2	55.6	77.8	34.5	72.4	56.0	52.0	45.5	47.8
	3	33.3	0	31.0	3.4	28.0	16.0	31.8	4.3
	4	0	0	6.9	0	8.0	4.0	4.5	4.3
	5	0	0	0	0	4.0	8.0	0	8.7
	6	3.7	7.4	13.8	3.4	0	4.0	9.1	13.0
	N =	27	27	29	29	25	25	22	23
Probability		0.000	0.005	0.071	0.000	0.172	0.000	0.022	0.000
Total N =		270	267	275	274	261	262	256	255

See legend, Tables 2 and 4.

Source : MNHN, Paris

The Functional Advantage of Proclined Incisors in Man

J. W. OSBORN, F. A. BARAGAR & P. E. GREY

ABSTRACT

The ways in which the spatulate incisors of higher primates can be used to help process food are described. Human upper and lower incisors are each tilted forward in the sagittal plane and the functional advantage of these forward inclinations is analysed by means of a biomechanical model (for the lower incisors) and a cine film of subjects biting into apples (for the upper incisors). The authors conclude that human upper and lower incisors are each tilted forward at the angle that maximizes their efficiency for cutting food rather than for the other ways in which spatulate incisors can be used.

RÉSUMÉ

Dans cet article sont décrites les diverses façons selon lesquelles les incisives spatulées des primates supérieurs peuvent être utilisées pour désagréger la nourriture. Chaque incisive humaine supérieure et inférieure est inclinée vers l'avant dans le plan sagittal; l'avantage fonctionnel de cette inclinaison antérieure est analysé au moyen d'un modèle biomécanique (pour les incisives inférieures) et d'un enregistrement cinématographique de sujets mordant dans une pomme (pour les incisives supérieures). Les auteurs concluent que les incisives humaines supérieures et inférieures sont inclinées vers l'avant d'un angle qui leur donne le maximum d'efficacité pour couper la nourriture, plutôt que pour toute autre action que peuvent exercer des incisives spatulées.

In: Teeth Revisited: Proceedings of the VII[th] International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 445-458.

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Source : MNHN, Paris

Introduction

The higher primates have two spatula-shaped incisors in each jaw quadrant, a design that distinguishes the group from nearly all other mammals. Within the group, however, the incisors have different sizes and arrangements, presumably associated with different functions. The present paper describes the different ways the incisors can be used and analyses the biomechanical efficiency of the arrangement in man.

Because they have only one set of replacement teeth, mammals face the necessity of developing a permanent dentition capable of withstanding a lifetime of tooth wear by abrasion and attrition. One strategy is to increase the size of the teeth. For example, the robust australopithecines have huge molars compared to those of other hominids, and also relative to the size of their own incisors. The large molars might be required to prolong their useful life or merely to provide the milling advantage of a broad working table suited to pulverizing small objects (Lucas *et al.*, 1985). The small incisors might have evolved in response to diminished use so that, for a given jaw size, the postcanine table captures space from the less used incisors. But a 2 cm span of incisal edge can produce double the pressure (force/unit area) of a 4 cm span having the same labio-palatal width, so that smaller incisors are not necessarily less used or less efficient than larger incisors.

The labio-palatal width of the incisors may provide some evidence of how they are used. A narrower incisor maintains a sharper cutting edge, when worn, than a broader incisor. The broad incisors of the recent great apes, when worn, divide food by crushing it rather than by cutting it (Fig. 1B). They may also be used with some precision to crush nuts for example (Fig. 1A), and as a grip to tear food apart in collaboration with the hands (Fig. 1F, G). Abrasion (tooth/food/tooth wear) could lead to cavitation of the dentine (Osborn & Lumsden, 1978) thereby providing a serrated grip like the jaws of household pliers but, unlike the occlusal surfaces of molars, the edges of incisors are rarely cavitated.

Upper incisors are usually much larger than lower incisors and have a broad cingulum. It is unlikely that this increased bulk is provided in order to compensate for wear because the lower incisors, when working against the uppers, must be subjected to the same amount of wear but they do not have a well developed cingulum. The broad cingulum may protect the palatal gingiva or provide a bigger anvil against which the lower incisors can work, either before the teeth are worn (Fig. 1C) or after they are worn (Fig. 1B). This type of " anvil " is worn into a band of soft dentine developed on the labial side of rodent upper incisors and has been discussed by Osborn (1969).

By means of attrition (tooth/tooth wear) it would be theoretically possible to sharpen incisors to work like a pair of scissors (Fig. 1D) in much the same way as carnassial teeth may be sharpened in carnivores (Lumsden & Osborn, 1977). But this sharpening mechanism does not seem to be used for the incisors of higher primates (it is used for the lingual surfaces of rodent lower incisors: Osborn, 1969). Man has maintained rather thin incisal edges and these can be used to cut (e.g. tailors cut cotton thread), but their edges are blunted by this process (Fig. 1E).

Many higher primates do have upper incisors worn into sharp edges by the removal of tooth substances from the palatal side. But the opposing lower incisors are also worn on their lingual sides. Such wear is presumably produced by husking and leaf stripping (Fig. 1H). Man uses a similar technique to remove food that has been previously impaled on a fork.

Most higher primates have an edge to edge incisor occlusion. This limits them to being used in the ways shown in Fig. 1A, B, F, G and H). Recent man has an overbite (the upper incisors overlap the lower incisors by about 1/3 of their crown height when the jaws are closed in centric occlusion) and an overjet (the incisal edges of the uppers are in front of those of the lowers) (Fig. 1C) so that the lower jaw must be opened and protruded to bring the upper and lower incisal edges together (Fig. 1E). The overbite and overjet allow man the opportunity of including in his repertoire the techniques shown in Fig. 1C and D. In heavily worn dentitions, however, the lower teeth tend to move forward and an edge-to-edge bite develops.

Source : MNHN, Paris

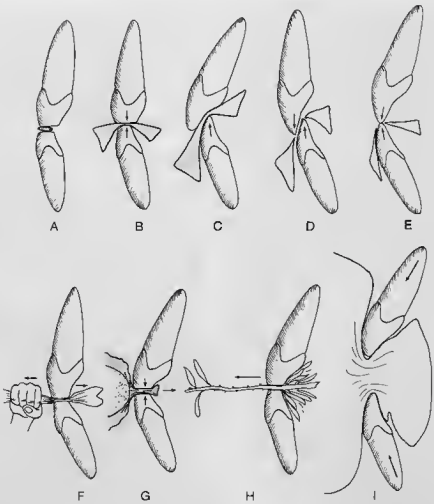

FIG. 1. — Diagrams representing the different ways in which the incisors of anthropoids could be used. Most techniques can be easily understood. G represents tearing meat off a carcass; H is stripping leaves; and I is biting into an apple.

MATERIAL AND METHOD

A. *Lower incisors*

We have investigated by means of a model the biomechanical efficiency of (human) incisors such as those shown in Fig. 1C in an attempt to understand the advantage of their forward proclination.

Previous work (Osborn & Baragar, 1985) has used a model to understand how the jaw muscles and teeth might combine to produce bite forces. Each jaw muscle, left and right, was divided into separate parts (4 parts for masseter [2 for deep and 2 for superficial masseter], 2 for medial pterygoid, 3 for lateral pterygoid and 3 for temporalis). The upper and lower attachments of each part were marked on a dried skull and their x, y and z coordinates measured in relation to a 3-dimensional reference frame. The xy plane passes through the mid-points of left and right condyles and is parallel to the occlusal plane. The xz plane is the mid-sagittal plane. The yz plane is perpendicular to the other two, and contains the mid-point of each condyle. Each part of each muscle was alloted a maximum possible tension, based on the work of Schumacher (1961) and Pruim *et al.* (1980). The positions of the centre of each condyle and of each tooth

Source : MNHN, Paris

were also given x, y and z coordinates. All data were entered into a computer file.

The mass of the jaw is so small and its acceleration during mastication is so little that equations for static equilibrium can be used to calculate the muscle forces, bite force and joint reaction forces. To produce a given bite reaction force (B) on a lower incisor in a particular direction (β) in the sagittal plane, and with an unknown joint reaction force of magnitude (J) acting in a given angle (μ), there are an infinite number of different combinations of muscle forces and joint reactions that will satisfy equilibrium conditions. Their resultant, M, must pass through the intersection of B and J (Fig. 2). One out of this infinite set of combinations requires less muscle force than any of the others and this unique combination can be found, with the aid of a computer, by using a linear programming algorithm (Campbell, 1977). A previous study (Osborn & Baragar, 1985) showed that the combination of muscle tensions selected in this way, as opposed to the combination that minimizes the joint reaction, is similar to that observed in EMG studies of man (Møller, 1966; Pruim *et al.*, 1980).

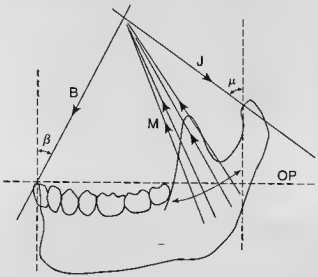

FIG. 2. — B, J and M are the bite reaction, joint reaction and the muscle resultant respectively. The interrupted lines are the occlusal plane (OP) and the normals to it that pass through the points at which B and J are applied to the jaws. All angles are measured anticlockwise with 0° being at the 12 o'clock position. Thus, in this diagram, the bite angle (β) is approximately −35° and the joint reaction angle (μ) is approximately +55°. Equilibrium conditions can only be satisfied if M, the resultant of the combined muscles of mastication passes through the intersection of B and J. An infinite number of different muscle combinations could satisfy this requirement (different arrows). Although the diagram represents only 2 dimensions, the model calculates the forces in 3 dimensions. (Note that the muscle resultant shown in this diagram is not the same as the sum of the muscle tensions. If two muscles each pull with 10 kg force in opposite directions then the sum of the muscle tensions is 20 kg but the magnitude of their resultant is zero).

For biting (in the midline) on the incisors the problem can be justifiably reduced to two dimensions. Suppose the joint reaction, generated between the condyle and articular eminence, is directed downward and backward at +55° to the vertical (the occlusal plane is defined as horizontal): and the reaction to the bite force is directed upward and backward at −35° to the vertical, in the midline on the lower central incisors (Fig. 2). The model can be used to calculate the maximum bite force that could be produced under these conditions. We can now vary the direction of the bite reaction or the direction of the joint reaction and find the combination that would produce the maximum possible bite force. It transpires (Fig. 3) that for each joint reaction angle an upward and backward bite angle of −20° (range −20° to +50°) enables the maximum bite force to be developed. For each point on the graph, no matter how the different muscle tensions were combined, there is no combination that would increase the bite force while maintaining equilibrium conditions.

The articular surfaces and disc of the mandibular joint have a very low coefficient of friction (Charnley, 1959). The joint reaction, therefore, must be perpendicular to a tangent to the articulating surface of the condyle because if it were at any other angle the condyle would be forced to slide and thereby break the conditions for equilibrium (Osborn & Baragar, 1985). In the sagittal plane the human mandibular condyle is gabled like the roof of a house (Rees, 1954; Scott & Dixon, 1972; Osborn, 1985) with its articular surface facing in the antero-superior direction (inset, Fig. 3). The fibrous tissue covering the articular surface is thin (0.25 mm to 0.5 mm: Hansson, 1977) so that the shape of the articular surface during life is almost the same as that of the bone surface that can be observed on a dried skull. This surface is flattened in the sagittal plane (Rees, 1954; Osborn, 1985) and tilted forward at between 15° and 30° to the occlusal plane (the occlusal plane is horizontal in our

Source : MNHN, Paris

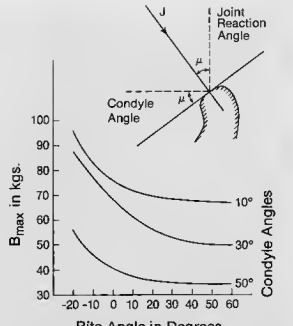

FIG. 3. — The maximum bite force (B_{max}) is plotted for different bite angles choosing +10°, +30° and +50° as condyle angles. The inset shows that the joint reaction angle (μ) equals the forward tilt of the articular surface of the condyle from the horizontal (condyle angle). The articular surface of the condyle is roughly parallel to the articular eminence.

coordinate system). The joint reaction angle (μ) equals the *condyle angle* (inset, Fig. 3), the angle at which the condyle is tilted forward from the horizontal (Osborn & Baragar, 1985). If the human jaws and dentition were designed to maximize the bite force that could be produced during incision, the results in Fig. 3 suggest the articulating surface of the condyle would be tilted forward at an angle less than 10°. Furthermore, the lower incisors would be tilted *back* at an angle greater than (minus) 20°, the angle at which the maximum bite force would be directed down the long axis of the tooth. We conclude that the human jaws and dentition are not designed to maximize the bite force in the incisor region.

A second biomechanical approach is to analyse the efficiency with which muscle tensions can be converted into bite force using different condyle angles and bite angles: that is, to measure the ratio of the input (the sum of all the muscle tensions = Σ M) to the output (the bite force = B) under different conditions. As before, the most efficient combination of muscle tensions is revealed by linear programming. From these data the total muscle tension is summed. It is not the same as the magnitude of the muscle resultant. For example, if two muscles pull with forces of 10 kg in opposite directions the muscle resultant is zero but $\Sigma M = 20$ kg. The efficiency is represented as a percentage figure ($(B \times 100)/\Sigma M$). For every condyle angle in the range 0°-50° (Fig. 4) there is a bite angle that can convert muscle tension into bite force with an efficiency of about 40 %. In the same way for every bite angle there is an equally efficient condyle angle. A study of the efficiency with which bite force can be produced does not therefore help us to understand the functional advantage of the orientation of human lower incisors and the articular surface of the condyle. For any given condyle angle (range 0° to +50°) it is always possible to select a combination of muscle tensions that produces a bite force that is about 40 % of the total muscle tension: and no arrangement that we studied can exceed this percentage.

A third approach to biomechanics is to calculate the efficiency with which muscle contraction is converted into work done by the lower incisors in moving through food. Under these conditions the direction in which the tooth actually moves must be considered.

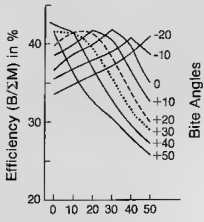

FIG. 4. — The efficiency of producing a static bite force of 10 kg is plotted against condyle angle for different bite angles. The interrupted and dotted lines are used merely to distinguish between lines that cross each other. There appears to be no functional advantage for any particular condyle angle. By choosing the appropriate bite angle all condyle angles are about equally efficient.

Source : MNHN, Paris

We assume that the lower incisors move in a direction (ψ in Fig. 5) that is tangent to the arc of a circle centred at the condyle. The bite force has two components, one in the direction of movement (double arrows in Fig. 5) and one directed through the centre of rotation on the condyle. This latter component is not shown in Fig. 5 because there is no movement in this direction and therefore no work (force × distance) can be done. The work done is therefore:

$$B\ d\ \cos\ (\psi\text{-}\beta) \qquad (i)$$

where d = the distance moved. For reasons related to the physiological effect (Carlson & Wilkie, 1974) of shortening a muscle on the tension it can produce, and the changes in ψ, and the changes in the directions of the muscle tensions as the lower jaw rotates during closure, d must be kept small for the purposes of calculations. However, if we are comparing the efficiency at doing work at a specified bite location (in this case, the tip of the lower incisor) using different condyle angles and bite directions, we can keep d constant and therefore ignore it when making comparisons.

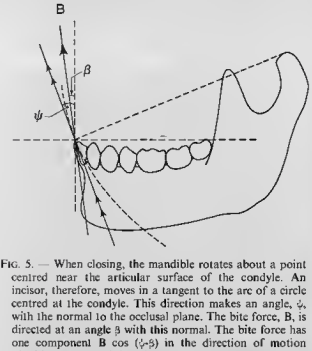

FIG. 5. — When closing, the mandible rotates about a point centred near the articular surface of the condyle. An incisor, therefore, moves in a tangent to the arc of a circle centred at the condyle. This direction makes an angle, ψ, with the normal to the occlusal plane. The bite force, B, is directed at an angle β with this normal. The bite force has one component B cos (ψ-β) in the direction of motion (double arrows) and the other component directed towards the condyle (not shown). There is no movement in this latter direction so no work (force × distance) is done by this component. Angles are measured in an anticlockwise direction with 0° being at 12 o'clock (e.g. 1 o'clock is —30° and 10 o'clock is +60°).

The work done by the incisor is at a maximum for a given B when $\psi = \beta$ because cos (ψ-β) in expression (i) now equals one, its maximum. The larger the angle between ψ and β the less of the bite force is converted into work. But the situation is complex because the jaw muscles do not necessarily combine most efficiently (Fig. 4) to produce a bite force in the direction ψ (which equals about +20° in man). We analyse efficiency by calculating the ratio B cos (ψ-β)/Σ M for different values of β and of μ (the condyle angle = the joint reaction angle). The results are shown in Fig. 6A. As with the results for static bite force (Fig. 4), the results for dynamic bite force (work) do not suggest a functional advantage for the observed human condyle angle (15°-30°) or the forward tilt of the lower incisors (about +20°). Other combinations of bite angle and condyle angle can produce work with similar or slightly greater efficiency.

We made similar calculations with the jaws opened and slightly protruded to separate the upper and lower incisor edges by 1.4 cm. The positions of all the muscle attachments to the lower jaw in relation to those in the upper jaw are changed by rotating the mandible with the result that the tension generated by each muscle is in a different direction from that when the jaws are in occlusion. These differences were calculated and new muscle directions employed. Some results are shown in Fig. 6B. Repeating the calculations using 20 kg instead of 10 kg forces had little effect on the results. As before, the results do not suggest a functional advantage for the observed human condyle angle or the tilt of the lower incisors.

We finally studied cutting efficiency. The efficiency of cutting is inversely proportional to the area of the cutting edge. A knife is more sharp when the surface of its cutting edge is smaller because for a given force the pressure (force/unit area) generated at the cutting edge is greater. To measure the efficiency of incisors cutting food we need to measure the surface area of the cutting edge.

Viewed in the sagittal plane, a lower incisor can be visualized as a rectangle whose long sides are the buccal and labial surfaces and whose tip is one of the short sides (Fig. 7a). The area of the " cutting edge " is the projection onto the plane perpendicular to the direction of movement of the area of that part of the incisor embedded in

Source : MNHN, Paris

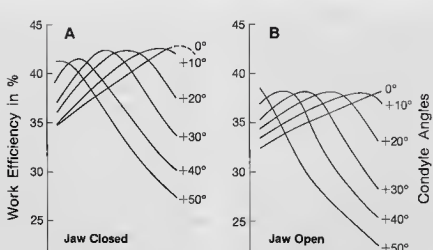

FIG. 6. — Work efficiency (dynamic bite force) using a 10 kg bite force is plotted against bite angle for different condyle angles with the jaws closed (A) or opened about 1.4 cm (B). There is no advantage for any particular condyle angle. For any condyle angle, a bite angle can be found that is nearly as efficient as the most efficient combination of other condyle and bite angles.

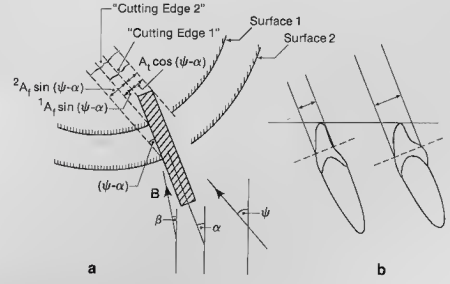

FIG. 7. — An incisor is represented as a rectangle in cross section (a). It moves in a direction ψ with a bite reaction B in a direction β. The long axis of the rectangle (incisor) lies at an angle α. The area of the tip of the incisor embedded in food is A_1 and of its buccal (or lingual) face is A_f. When the rectangle has penetrated a short distance into an apple (surface 1) its " cutting edge " has a cross sectional area $A_1 \cos(\psi-\alpha) + {}^1A_f \sin(\psi-\alpha)$. With further penetration (surface 2) the " cutting edge " is enlarged to $A_1 \cos(\psi-\alpha) + {}^2A_f \sin(\psi-\alpha)$.
When 3/4 embedded in an apple (b), for example, an incisor with a cingulum cuts much less efficiently than one without a cingulum because its " cutting edge " is so much larger.

Source : MNHN, Paris

the object being cut. A_t is the area of the tip and A_f is the area of the face of the incisor embedded in the food being cut (Fig. 7a); ψ is the direction the tooth is moving and α is the orientation of the long axis of the tooth (rectangle). The area of the "cutting edge" facing in the direction of movement is $A_f \sin(\psi-\alpha) + A_t \cos(\psi-\alpha)$. If the bite force B is in a direction β, the average pressure (P) at the "cutting edge" is given by:

$$P = \frac{B \cos(\psi-\beta)}{A_f \sin(\psi-\alpha) + A_t \cos(\psi-\alpha)} \qquad \text{(ii)}$$

If $B \cos(\psi-\beta)$, the force driving the incisor into the food, is kept constant the different magnitudes of P for different variables in the denominator can be used to compare cutting efficiencies: the bigger the value of P, the greater is the pressure and the greater is the efficiency. Thus, efficiency is inversely proportional to the denominator of equation (ii).

At the end of a pure rotary movement the lower incisor is moving at an angle of about +20° to the occlusal plane (tangent to the arc of a circle centred at the condyle: Fig. 5). Thus ψ = 20° and we can substitute a single variable $\chi = (20°-\beta)$ for $(\psi-\beta)$ in equation (ii). The cutting efficiency at this terminal position is, as always, related to the amount of tooth already embedded in the food. For example, if only 1/3 of the tooth is embedded in the food (surface at 1 in Fig. 7a), the "cutting edge" is much smaller than if 2/3 of the tooth is embedded (surface at 2 in Fig. 7a). Suppose now that the embedded profile of the incisor has dimensions such that $A_f = 10\ A_t$. Because A_t is small in relation to A_f the minimum value of the denominator in equation (ii) is roughly A_t; that is, when $\psi = \alpha$ and the tooth is moving in the direction of its long axis (so that $A_f \sin(\psi-\alpha) = 0$). The effect of χ on cutting efficiency when $A_f = 10\ A_t$ is shown in Fig. 8. If χ is 10°, the cutting edge is 3 times the area when χ is 0° (3 on the ordinate of Fig. 8). Thus, if $\chi >$ 10° the efficiency of cutting is reduced by at least a factor of 3.

The work done by the "cutting edge" in moving through food is directly related to B cos

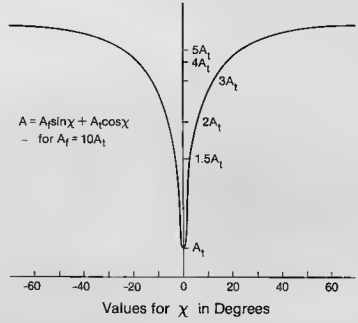

FIG. 8. — The efficiency of cutting depends on the pressure (force/unit area) that is applied to the cutting edge. The area of the "cutting edge" of a rectangle (Fig. 7a) is related to the amount embedded (e.g. at surface 1 or 2), its orientation and the direction it moves in relation to the object being cut: $(\psi-\alpha) = \chi$. Cutting efficiency is inversely related to the area of cutting edge embedded in the food. Suppose the part of the face of the rectangle embedded in the food is 10 times the area of its tip ($A_f = 10\ A_t$). The area of "cutting edge" varies with χ. The smaller the value of χ, the greater the efficiency. If χ is 0° (the rectangle is moving in the direction of its long axis) the area of the cutting edge is that of its tip and equals A_t (see value of ordinate for $\chi = 0°$). If $\chi = 10°$ the surface of the cutting edge is 3 times greater (if $\chi = 10°$ the value on the ordinate is 3 A_t).

Source : MNHN, Paris

(ψ-β), the force in the direction the tooth is moving (see Fig. 5 and expression i). The efficiency with which the jaw muscles can produce this work, for different values of β and the condyle angle (μ) is shown in Fig. 6. With widely different values of β and μ the maximum efficiency varies between 30 % and 40 %. But for values of χ greater than 10° the denominator of expression (ii) is at least 3 times greater than its minimum value A_t. It seems clear that the value of χ, compared with those for β and μ, provides by far the most important contribution to the cutting efficiency of lower incisors. The calculation that P is near its maximum when $\psi = \alpha$ (Fig. 7a) may therefore explain the advantage for commonly orienting human lower incisors roughly parallel to a tangent to the arc of a circle centred at the condyle; that is, making α approximately 20° because ψ is approximately 20° and therefore χ is approximately 0°.

We do not know whether, at the beginning of incision, the jaw muscles are necessarily rotating the incisors along the arc of a circle centred at the condyle and therefore that the incisors are most efficiently oriented for cutting the food. When the lower incisors begin penetrating food A_f is not much larger than A_t (say $A_f = 2\ A_t$) with the result that Fig. 8 does not accurately represent efficiency in terms of χ (for this figure $A_f = 10\ A_t$). The further the incisors penetrate into the food, the larger A_f becomes in proportion to A_t (Fig. 7a) and the more sharply delineated becomes the apex at $\chi = 0°$ in Fig. 8. It seems possible that periodontal receptors for the lower incisors might, via central connections, cause the change in muscle tensions which would drive the lower incisors into the food at the angle that minimizes the resistance to their movement. This would bring χ near to 0°. We suggest, however, that the observed tilt of the lower incisors (the angle α in Fig. 7a) is a direction in which the muscles of mastication do move the lower incisors during incision: the actual centre of jaw rotation can be moved a little distance away from the condyle by simultaneously translating the jaw (moving the condyle up or down the articular eminence).

This analysis suggests a functional advantage for the absence of a well developed cingulum on lower incisors. Were a cingulum present the cutting efficiency of lower incisors would be reduced: an incisor with a cingulum half buried in food (Fig. 7b) is cutting perhaps half as efficiently as one without a cingulum (the area of the "cutting edge" is about doubled).

We conclude that the lower incisors in man lack a cingulum and are oriented in roughly the direction they move during jaw movement because this anatomy and arrangement produces the most efficient cutting mechanism. Lower incisors (and the mandible and jaw muscles) are *not* designed (i) to maximize the bite force in the incisor region, (ii) to maximize the efficiency with which bite force is produced here, or (iii) to maximize the efficiency for doing work here. In a previous study (Baragar & Osborn, 1987) we have shown that human lower molars are designed and oriented to maximize their efficiency for doing work (dynamic bite force) and *not* to maximize the bite force they can produce or their efficiency at producing static bite force.

B. *Upper incisors*

Human upper incisors are oriented within the sagittal plane at a quite different angle from that of the lower incisors. This suggests they do not merely provide a resistance for the lower incisors, otherwise they would probably be retroclined (in line with the lowers) — as they indeed are in some mammals. We investigated the way in which upper incisors are used in man, by means of a cine-film study of subjects biting into an apple.

Eight subjects biting into an apple were viewed from the side and filmed with an 8 mm cine camera (Fig. 9). A head gear with anterior and posterior extensions was positioned on a subject in order to study the movement of the upper incisors. Although the teeth were obscured while they were penetrating the apple their movement could be analysed by reference to the markers attached to the head gear. The movement of the apple itself was visualized by sticking into it an 8 inch long pin. The head of the pin and the point where it penetrated the apple acted as markers. Black paper spots were stuck to the tip of the nose, the point of the chin and the skin over the mandibular condyle to assist analyzing the movements.

A chair with a back rest was placed sideways close to a white wall. Each subject was instructed to sit upright in the chair, facing directly forward

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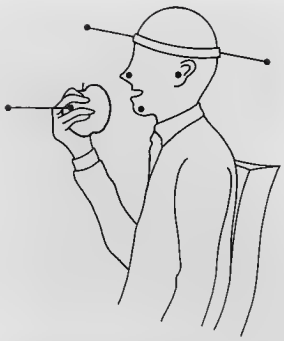

FIG. 9. — Marker points were attached to the front and back of the head gear, to the head and base of a pin stuck into the apple, and to the nose, chin and skin in front of the ear.

with the back firmly supported by the back rest, and to avoid moving away from this support or turning the head to left or right while taking bites out of the apple. With these restrictions subjects were asked to eat the apple as normally as possible, repositioning the pin for each bite.

Subjects were filmed at speeds of 16 frames per second. Each was filmed 5 or 6 times depending on the number of bites required to work around the perimeter of the apple. As successive films were projected at slow or normal speeds it became increasingly easy to understand how the subjects were using their dentitions to bite into the apple. We allowed these somewhat subjective impressions to direct our subsequent, more objective, analysis of the movements.

Single frames of the developed films were projected on a wall with a resultant magnification of about × 3/4. The frames chosen for the analysis were those which coincided with a clear change in the direction the head was moving. All markers and what could be seen of the facial profile (partly obscured by the apple) were traced on paper.

Although several measurements of the tracings were made it transpired that there were so many minor variations in behaviour that a detailed analysis would obscure the overall, very obvious picture.

Biting an apple involved three separate phases: preparation, biting and recovery.

1. PREPARATION.

As the apple was raised towards the mouth the upper incisors were usually hidden by the upper lip but their movement in relation to the background could be assessed by the movement of the markers attached to the head and the facial profile. They generally moved upwards and forwards but one subject (B) moved his head downwards and forwards while another (F) moved very little (Fig. 10). In some subjects the movement was more vertical and in others it was more horizontal. By reference to the markers attached to the head gear (the front marker moved up and the back marker moved down) it could be demonstrated that the vertical component was largely achieved by rotating the head on the cervical vertebral column (contracting the post-vertebral muscles).

2. BITING.

This consisted of two overlapping phases, upper and then lower.

Upper Biting.

The upper incisors moved downwards and forwards and then into the apple (Fig. 10). The amount of the horizontal component of this movement varied between individuals: occasionally the movement seemed almost vertical but usually the angle was between 40° and 20° to the vertical. By reference to the markers on the head gear we could estimate an approximate centre of rotation (Fig. 11). This usually lay between 2 to 5 cm in front of the cervical vertebral column between the levels of C_1 to C_3 (Fig. 12). The size of this region indicates the considerable variation between subjects (and for each particular subject).

The movement of the apple was monitored by the movement of its profile. Three subjects (B, D and E in Fig. 10) appeared to hold the apple stationary in the vertical plane, two (A and C) allowed it to move down while one (F) moved the apple up into the upper incisors. By reference

Source : MNHN, Paris

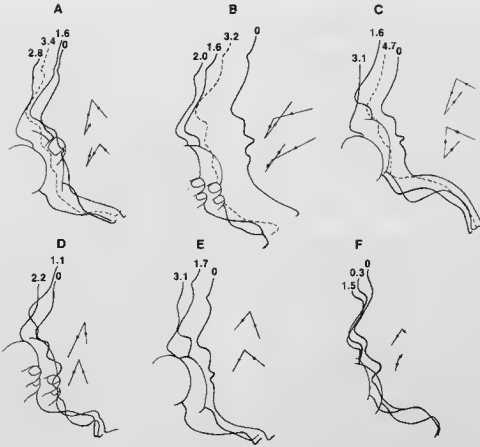

FIG. 10. — Each sequence of tracings shows the movement of the head while taking a bite out of an apple. The four tracings in each of A, B and C indicate the start, the change from preparation to biting phase, from biting phase to recovery, and some point within the recovery phase (indicated by an interrupted line). The figures show the time in seconds from the start (time 0) calculated from the frame numbers (16 frames/sec). The lower set of arrows show roughly the movement of the upper incisors that corresponds with the tracings. The upper set of arrows show the incisor movements of the same subject during a different sequence. The recovery phase has been omitted from D, E and F. The thumb or fingers covered the profile of the apple for 3 subjects (A, B and D). Subject A changed his grip on the apple during the biting phase.

to the markers on the apple it could be shown that, although the apple was usually moved little in the vertical plane, it often rotated clockwise (subjects were viewed from the left) probably due to a force couple developed between the downward drive of the upper incisors and the upward push provided by the resistance of the hand holding the opposite side of the apple (Fig. 11). We have subsequently observed an individual who seemed to keep his head stationary during the upper biting phase, all the relative movement being achieved by pushing the apple into the upper incisors.

Lower Biting.

After the upper incisors had begun penetrating the apple the lower jaw was closed, driving the lower incisors into the apple. The combined forces acting on the apple from upper and lower teeth and from the hand caused different and unpredictable movements of the apple during lower biting (Fig. 11).

3. RECOVERY.

Biting ended when the head was moved backwards and upwards away from the apple and the hand was lowered (Fig. 9). Differences between the size of the bites and the speed of ingestion led

Source : MNHN, Paris

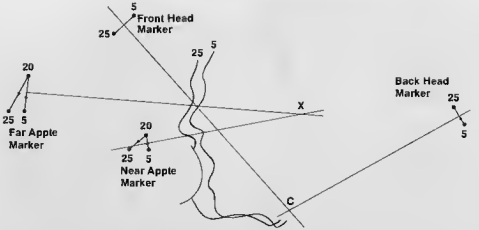

FIG. 11. — The movements of the markers attached to the head gear and the apple during the biting phase are shown. The front head marker moved downwards and forwards between frames 5 and 25 (16 frames/sec) while the back head marker moved upwards and forwards. Perpendicular bisectors of each traverse meet a point C, the head's approximate 'centre of rotation' for this sequence. The front and back markers on the apple moved less regularly. During the upper biting phase (frames 5 to 20) it was rotated clockwise about the point X. During the lower biting phase (the last 5 frames) the apple moved downwards and forwards.

us to describe subjects as between "cautious deliberate biters" (subject F with 1.2 seconds for the power stroke) and "aggressive decisive biters" (subject B with 0.4 seconds).

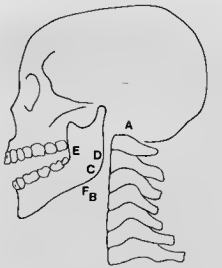

FIG. 12. — The approximate centres of head rotation during the biting phase for each subject are shown. That for subject A apparently had an abnormally high centre of rotation.

We have already concluded that the long axes of human lower incisors are roughly tangent to the arc of a circle centred at the jaw joint, the direction in which they move when the jaw is being closed, because this maximizes their cutting efficiency.

The present study showed that the upper incisors also move through an apple roughly in the direction of their long axes. The impression of the upper teeth left in the bitten surface indicated they had done work by moving through the apple. Much of this work can only have been done by prevertebral muscles. Amongst these, sternomastoid has the longest moment arm while rectus capitis anterior aids flexion at the atlanto-occipital joint and the scalene muscles help flex the remainder of the cervical column. Sometimes work was done by the arm pushing the apple up into the upper incisors, the potential displacement of the head being resisted by the prevertebral muscles. It is worth mentioning that the forward displacement of the head on the vertebral column during the phase of preparation increased the length of the moment arm of sternomastoid with respect to the cervical vertebral column during the phase of biting.

Ligaments and bony constraints severely limit the amount by which the cervical vertebral column can be flexed. The atlanto-occipital joint,

Source : MNHN, Paris

however, can be flexed 40° (Joseph, 1982). Therefore the centre of rotation for flexing the head must commonly be in front of and toward the upper end of the cervical vertebral column. The long axis of the upper incisors is in a direction roughly tangent to the arc of a circle centred here. And this was the direction moved by the upper incisors in the present study.

The clearest conclusion from the cine film study is that the cervical vertebral muscles are used as muscles of mastication that move the upper teeth. The generally described muscles of mastication only move the lower teeth. We would be guilty of sophistry to argue that movement is merely relative so that masseter, for example, can be considered to move the upper jaw in relation to the lower. For static bite forces the argument is reasonable, but not for dynamic bite forces.

We do not know whether the upper incisors are proclined at the angle that most efficiently converts muscle force, provided by the prevertebral muscles, into dynamic bite force (work) at their incisal edges. This would require an extensive study such as that undertaken for the lower teeth, including an analysis of the joint reactions in all the articulations of the cervical vertebrae (as opposed to the two joints on the mandible needed to analyse the efficiency of lower teeth). Nevertheless we conclude that both upper and lower incisors in man are designed and oriented to maximize their cutting efficiency (Fig. 1E, I). Their different orientations are required because during cutting each rotates about a different axis — the condyle for the lower incisors, and some point in front of the upper part of the cervical vertebral column for the upper incisors.

It remains to account for the well developed cingulum on human upper incisors. The arguments related to Fig. 7b indicate that a well developed cingulum severely reduces cutting efficiency when the cingulum has become embedded in the food being cut.

The presence of a cingulum on the upper incisors may be important to widen the repertoire of uses to which the incisors can be put. As described earlier, the cingulum acts as an anvil against which the lower incisors can work (Fig. 1C). Two different types of secateur are used for pruning trees; one has a blade and anvil and the other has two blades. The former cuts thinner branches more efficiently and the latter is more efficient with thicker branches. This difference is related to the resistance to cutting rather than to size. Thus, thinner more resistant food such as tough meat may be more effectively cut by blade and anvil (lower incisor edge and upper incisor cingulum: Fig. 1C): the upper incisor cingulum is not required to penetrate thin food. Thicker or less resistant food is more effectively cut by blades (upper and lower incisal edges: Fig. 1E, I). It should be noted that to be able to use both types of cutting requires the upper incisors to be in front of the lower incisors. In this position blade and anvil cutting is used. For blade/blade cutting the lower jaw must now be protruded.

Most higher primates have an edge to edge incisor relationship. With the exception of the activity represented in Fig. 1H, incisor wear rapidly blunts their edges and food is then cut by brute force, by crushing (Fig. 1B) rather than cutting. The worn incisors provide a better grip (Fig. 1F, G) than unworn incisors. The incisors can also be used as a third hand, for gripping. This activity blunts the incisor edges and improves their grip.

We have provided evidence elsewhere (Baragar & Osborn, 1987) that the human jaws and postcanines are probably designed to maximize the efficiency with which muscle force is converted into work done by the molar teeth. This establishes the shape of the condyle in relation to muscle design, neither of which is particularly suited to incisor function. Human incisors are so designed and oriented that they can undertake a repertoire of activities, not all of which may be employed by a particular culture. Each activity makes use of existing jaw and muscle design that during evolution was probably focused more on improving molar efficiency.

Conclusion

In an earlier study of the human dentition Baragar & Osborn (1987) showed for each molar that if the bite force is directed down its long axis, tilted forward in a direction conforming with the curve of Spee, the work done by that molar is maximized. In contrast, the maximum bite force and the efficiency at which static bite

Source : MNHN, Paris

force can be produced are both less than those which could be produced by a more vertical orientation. We have now repeated these studies for human lower incisors. Neither the maximum bite force, nor the efficiency at which the bite force is produced, nor the efficiency for doing work are maximized by directing the bite force down the long axis of a lower incisor tilted forward at its observed angle of about 20° to the occlusal plane. This angle, however, maximizes the efficiency with which food can be cut.

Observations of subjects biting apples show that the head is moved in such a way that the upper incisors are driven into the apple in a direction roughly down the long axis of the upper incisors. This direction is tangent to the arc of a circle centred somewhere slightly in front of the upper cervical vertebrae and is the centre about which the head normally rotates when flexing the neck. In other words, the upper incisors are tilted forward at an angle that maximizes their cutting efficiency when the head is flexed.

We conclude that human upper and lower incisors are proclined in the jaws at angles that maximize the efficiency with which each can be used to cut food.

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Isometric Scaling of Mammalian Cheek Teeth is Also True Metabolic Scaling

M. FORTELIUS

ABSTRACT

The rate of food comminution depends on the amount of food comminuted per chew and the chewing rate. It is suggested that the former scales isometrically with the volume of food enclosed between the cheek teeth, rather than directly with occlusal area, as proposed previously. Chewing rate appears to scale with body mass to the power — 1/4. Thus comminution rate would scale with metabolic rate, as body mass to the power 3/4. This would resolve the apparent paradox of predicted positive allometry and observed isometry of mammalian cheek tooth area. Some implications of the model are discussed. It is proposed that occlusal morphology is the one functional factor that is size-independent, and that the radiation of mammalian cheek tooth morphology is largely a result of this independence.

RÉSUMÉ

Le taux de désintégration de la nourriture dépend de la quantité de nourriture désagrégée par mouvement masticatoire, et du rythme de la mastication. Le premier facteur paraît dépendre du volume de nourriture enfermé entre les dents jugales, plutôt que de leur surface occlusale, comme cela avait d'abord été proposé. Le rythme masticatoire semble proportionnel à la masse du corps élevée à la puissance — 1/4. De la sorte, le taux de désintégration suivrait le taux métabolique, comme par conséquent la masse du corps, à la puissance 3/4. Ceci résoudrait le paradoxe apparent entre la prédiction d'une allométrie positive et l'observation d'une isométrie pour la surface des dents jugales mammaliennes. Quelques implications du modèle sont discutées. Il est proposé que la morphologie occlusale constitue le seul facteur fonctionnel qui soit indépendant de la taille, et que la radiation de la morphologie des dents jugales mammaliennes est largement le résultat de cette indépendance.

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Introduction

In two highly stimulating and influential papers, Pilbeam & Gould (1974), and Gould (1975) proposed that mammalian teeth should scale with positive allometry to body size in order to satisfy metabolic needs. To be precise, they suggested that postcanine occlusal area should scale as metabolic rate with body mass to the power 3/4 (instead of the 2/3 signifying geometric similarity). Since then many authors have shown that postcanine teeth are in fact isometric to body size in the overwhelming majority of the cases studied (Kay, 1975, 1978; Lucas, 1980; Creighton, 1980; Prothero & Sereno, 1982; Gingerich *et al.*, 1982; Fortelius, 1985; Janis, this volume). A conflict thus exists between theoretical predictions and the observed data. I have recently proposed a resolution of this paradox (Fortelius, 1985), but since this may have been hidden within the monograph of which it formed part, I feel justified in presenting a somewhat amended and simplified version here. I provide no new data, but discuss some implications which I did not consider in the original version.

This is not the context to enter into speculations about the reason(s) for the widely observed scaling of metabolic rate to body mass as $M_b^{3/4}$. For a lucid discussion of proposed explanations see Schmidt-Nielsen (1984). It may be pointed out, however, that biologists so far have paid relatively little attention to the scaling of time parameters, and that success may well lie in that direction. In the following I will take the metabolic exponent 3/4 as given.

Basic considerations and the model

It would be unnecessary to discuss the fairly well known model proposed by Pilbeam & Gould (1974) in detail here; the interested reader may consult the original papers and Fortelius (1985). For the present purpose it is sufficient to present the alternative.

Let us begin with basic considerations. Food must be processed to meet metabolic needs, i.e., in proportion to $M_b^{3/4}$. The mass of food comminuted per unit time must depend on (i) the mass comminuted per chew and (ii) the chewing frequency. Gould & Pilbeam (1974) thought that (i) would scale directly with postcanine occlusal area, for isometric animals as $M_b^{2/3}$. This assumes that the food between the teeth is of unit thickness from mouse to elephant, which seems unlikely. I suggested (Fortelius, 1985) that the volume enclosed between occluding teeth of isometric animals would, for any given food and occlusal morphology, be isometric to body size, and that the volume comminuted per chew would scale similarly as M_b^1.

This suggestion receives some support from recent findings by Lucas *et al.* (in press), which seem to indicate that the volume perceived is the decisive variable in determining both vertical jaw movements during chewing and swallowing (at least in humans). Chewing results in successively reduced food particle size and thus in a successively smaller volume. After a sufficient number of chews the volume reaches a value at which swallowing is triggered. Absolute size does not seem important, as initial particle size does not influence the result (Lucas *et al.*, in press). This view is at least consistent with recent detailed analyses of mastication, food transport and swallowing in several species of mammals (Hiiemäe & Crompton, 1984).

It seems reasonable to speculate that animals ingest some approximately optimal mouthful of each food, and chew until it has been sufficiently reduced in volume. For each occlusal design and food type, the number of chews would then be constant and independent of absolute size. (For a detailed discussion of food comminution, see Fortelius, 1985, and references therein).

Data on chewing frequencies are surprisingly rare. What little is available suggests that chewing frequency depends on body size as do most physiological rates, approximately as $M_b^{-1/4}$ (Fortelius, 1985). If volume comminuted per chew is isometric to body size and chewing frequency scales as $M_b^{-1/4}$, food comminuted per unit time will then scale as $M_b^1 \times M_b^{-1/4}$, or as $M_b^{3/4}$, i.e., as metabolic rate. If this is correct, isometric scaling of teeth is in fact also true metabolic scaling, and the apparent conflict between theory and data disappears.

The model requires that jaw muscles should also be isometric to body size. Only then will the critical parameter of occlusal stress remain independent of body size, which is more or less

Source : MNHN, Paris

necessary if the model is to work. The reason is, that muscular force is proportional to cross-sectional muscular area or $M_b^{2/3}$, which is also the scaling of occlusal area. Occlusal stress is force per area, for isometric animals proportional to $M_b^{2/3} \times M_b^{1/2} = M_b^1$. Data are scarce, but it is reassuring that Cachel (1984) found isometric scaling of the jaw muscles in a wide selection of primates.

The model is strictly testable only for recent mammals, since chewing cannot be observed in fossils. For the latter, one has to be content with the observation that it explains (is consistent with) the observed isometry.

Discussion

It may be relevant to recall that Pilbeam & Gould (1974) originally developed their argument about " metabolic " scaling to account for the differences in relative size of the molars of gracile and robust australopithecines. Their well-known conclusion was that differences signify no more than functional similarity. If the re-interpretation presented above is correct, it follows that their conclusion is invalid, and that the functional implications of not only morphological but also plain size differences might be considered. The problem is more complex than it might appear at first sight, however, and I will leave it to those better qualified for the task.

It is extremely rare for growth to be isometric, and growth constraints are probably largely responsible for the allometric relationships between tooth size and body size generally found at intra-specific or even intra-generic levels (Fortelius, 1985). As a matter of fact, the whole discussion of the recent decades has been so allometry-oriented that the theoretical validation of isometry as functional similarity may seem anticlimactic. But for those who feel disappointed, there is the obvious compensation that general isometry is a very simple baseline for comparisons (criterion of subtraction *sensu* Gould, 1975). It should be emphasized, however, that dental isometry is not a phenomenon of low taxonomic levels, and that application of the criterion to closely related species (such as the different australopithecines) may be misleading. It is a strong possibility that differences between closely related species reflect growth patterns as much as or more than they do functional requirements.

As to mastication and food comminution, an interesting possibility suggests itself. If tooth size and chewing rate are determined by simple size-relations, dietary adaptations might be expected to affect primarily the parts of the process that determine food comminution during one chew, i.e., occlusal morphology and associated features of the mouth (such as the tongue). Particularly important aspects would be control of food breakage, flow and loading. One might even claim that the adaptive radiation of mammalian cheek tooth morphology itself has resulted mainly from this need to control food comminution during one single chew.

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This series of international symposia on the subject of dental morphology began in 1965. The meetings, covering a broad spectrum, have continued to be held since then with a periodicity of every three years.

The present symposium, the 7th of the series, was the first to be held in France. Distinguished specialists read contributions extending from Lower Vertebrates to Man and provided stimulating discussions on subjects as diverse as tooth germ initiation and the evolution of herbivory. The 34 articles presented here are accordingly distributed in 4 chapters : Embryology and Genetics, Evolution of Dental Tissues, Dental Morphology and Evolution, and Diet and Tooth Wear. While offering up-to-date views of the many aspects treated, these articles underline the inexhaustible nature of teeth as a resource for scientific research.

Donald E. RUSSELL is Directeur de Recherche au C.N.R.S. and a student of early Tertiary mammals. J.-P. SANTORO, Professor at the René Descartes University (Paris V) is a specialist of histology and physiology as applied to the masticatory system and to human nutrition. Denise SIGOGNEAU-RUSSELL, Chargée de Recherche au C.N.R.S., concentrates on the morphology and ultramicroscopy of the teeth of the first mammals.

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